ABSTRACT

Title of Thesis:	SPATIAL AND TEMPORAL DYNAMICS OF LARVAL ATLANTIC MENHADEN ON THE EAST COAST OF THE UNITED STATES
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Atlantic Menhaden *Brevoortia tyrannus* is a commercially and ecologically important forage fish abundant on the Atlantic Coast of the United States. We conducted spatial and temporal analyses of larval Atlantic Menhaden using data collected from two large-scale ichthyoplankton programs during 1977-1987 and 1999-2013 to construct indicies of larval abundance and survival over time, evaluate how environmental factors affect early life survival, and examine how larvae are distributed in space to gain knowledge on spawning and larval dispersal. Over time, we found larval abundance to increase, while early life survival declined. Coastal temperature, wind speed, and Atlantic Multidecal Oscillation were found to potentially explain some of this decline in survival. Over both periods, we found evidence spawning predominantly occurs near shore, from New York to North Carolina, increasing in intensity southwards. While the general spatial patterns were consistent, we observed some localized variation and overall expansion of occupied

area by larvae.

SPATIAL AND TEMPORAL DYNAMICS OF LARVAL ATLANTIC MENHADEN ON THE EAST COAST OF THE UNITED STATES

By

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Chapter 1: Introduction

Although not a well-known species to the general public, some believe Atlantic Menhaden *Brevoortia tyrannus* to be the most important fish in the sea (Bruce 2007). This claim, though grandiose, is not baseless. Ecologically, Atlantic Menhaden are an important forage fish and prey species to a variety of predators along the Atlantic Coast (Ahrenholz 1991). Economically, Atlantic Menhaden, with their Gulf counterpart, make up the second largest commercial fishery in the United States (NMFS 2014). Historically, the Atlantic Menhaden fishery is also one of the oldest, with some level of fishing occurring since colonial times and a large scale purse seine, reduction fishery since the mid-19th century (Reintjes 1969).

Atlantic Menhaden make up a single coast-wide population from Nova Scotia, Canada, to northern Florida, USA (Lynch et al. 2010). In the warmer months, adults occupy coastal waters and stratify by age, with the oldest, largest fish furthest north. As temperatures cool, Atlantic Menhaden undergo a seasonal southward, winter migrations (Reinjes 1969). Larvae are spawned and hatch in the coastal oceans and are transported into estuaries where they continue to grow and metamorphose into juveniles (Ahrenholz 1991). The Chesapeake Bay has been historically thought the primary nursery habitat for juvenile Atlantic Menhaden, hosting approximately 69% of the stock's recruits (Ahrenholz et al. 1989, ASMFC 2004). However, more recent research has suggested a lower and more variable contribution between 25 and 59% (Anstead and Jones 2014).

The Atlantic Menhaden population historically experienced high fishing pressure. Although once a coast-wide fishery, of the 25 processing plants (reduction fishery) that

were in operation during the fishery's peak in 1957 (SEDAR 2015), the only remaining factory operates in the Chesapeake Bay and continues to support the largest fishery on the U.S. Atlantic coast (NMFS 2014). In addition to the reduction fishery, the Atlantic Menhaden fishery also includes a bait fishery, which makes up ~23% of the total catch in the most recent years (SEDAR 2015). Peak commercial fishing activity occurred in the 1950s and 1990s in the southern range of Atlantic Menhaden, while the bait fishery peaked in the 1990s and early 2000s (SEDAR 2015). Yet, even with such high ecological and economic value, the processes controlling their recruitment dynamics remain elusive. In this work, we are focusing on the commercial sector of the industry, although the bait fishery is growing in value.

Biomass estimates are fairly constant through the 1970s and 1980s, but the stock reached an all-time low in biomass in the mid-1990s at 667,000 mt (SEDAR 2015). The fishery shrank dramatically during this period, with commercial landings decreasing from 401,200 mt in 1990 to 171,200 mt in 1999 (SEDAR 2015). Similarly, after a series of high recruitments in the 1970s and 1980s, recruitment declined coast-wide in the 1990s, and has remained stable during the 2000s with two strong year classes in 2005 and 2010 (SEDAR 2015). These strong year classes are generally from outside of the Chesapeake Bay, where low recruitment has been of particular concern because of a notable decline in age-0 recruitment in the Maryland seine survey since the 1990s (ASMFC 2010).

Recruitment processes for a migratory species with such a large spatial range are extremely complex and likely to vary both spatially and temporally (e.g. Quinlan et al. 1999). Likely causes for changes in recruitment can be classified by the impacted life stage (Houde et al. 2011). First, declines in the adult population from overfishing could

decrease spawning activity and thereby the amount of recruitment. Second, eggs and larval fish could be experiencing unfavorable oceanic conditions leading to increased early life mortality or transport failure. Finally, estuarine-dependent juveniles may be facing poor nursery conditions, like increased predation or poor water quality, causing increased juvenile mortality. My thesis predominately examines the second explanation for recruitment, as outlined by Houde et al. (2011), early life mortality and transport failure consistent with unfavorable oceanic conditions.

Atlantic Menhaden recruitment is highly variable, up to a 13 fold variation between consecutive years (Vaughan and Merriner 1991). At least part of this variability is due to environmental conditions. Temperature influences timing of spawning (Stegmann and Yoder 1996; Stegmann et al. 1999), transport (Epifanio and Garvine 2001), development, and survival and may be an important factor for early life survival of Atlantic Menhaden. Increased freshwater flow events from the Chesapeake Bay may influence larval transport from spawning grounds near Chesapeake Bay southward (Quinlan et al. 1999). Additionally freshwater flow could lead to higher recruitment in Chesapeake Bay (Kimmel et al. 2009) due to a potential increase of planktonic prey such as copepods (*Eurytemora affinis*; Houde et al. 2009). Large climate-scale patterns, such as the Atlantic Multidecadal Oscillation (AMO) could also be driving recruitment variation (Rice et al. 1999, Wood and Austin, Buchheister et al. *In Review*). Differences in circulation patterns on a multidecadal scale could have an effect on both where spawning is occurring but also where eggs and larvae are being transported along the Atlantic Coast.

Given the large distribution of the Atlantic Menhaden population in space,

individuals are exposed to a large range of environmental conditions. Juveniles are found in coastal estuaries from Georgia to New England (SEDAR 2015). While recruitment to nursery habitats is often correlated to other near-by habitats, patterns are not uniform along the Atlantic coast (SEDAR 2015). Specifically, recruitment to Southern New England estuaries has been found to be inversely correlated with several Mid Atlantic Bight estuaries (Buchheister et al. *In Review*). More work is required to determine whether such spatial variation in recruitment is due changes in spawning behavior or spatially varying early life survival.

Many species on the Atlantic coast have undergone shifts in larval abundance both spatially and temporally over the past several decades (Walsh et al. 2015). Because Atlantic Menhaden spawn coastally and are dependent on seasonal cues for an annual migration, changing coastal conditions could have major effects on the spatial distribution and transport of larvae. However, we do not have a complete understanding of Atlantic Menhaden early life history. Spawning aggregations have not been observed in the wild (Epifano et al. 2001) and most of what we know of spawning behavior comes from localized studies (e.g., Keller et al. 1999, Warlen et al. 2002, Light and Able 2003). Additionally, there is some debate on how larvae are transported in the system, across-shelf (e.g., Nelson et al 1977), along-shelf (e.g., Checkley et al. 1999), southward (Quinlan et al. 1999), or northward (Warlen et al. 2002).

My research provides more information on the early life stage of the species through the analysis of two spatially and temporally robust ichthyoplankton sampling programs. The primary goals of my first research chapter were to 1) track Atlantic Menhaden larval abundance over time and to 2) associate variations in early life survival

with several environmental factors. In order to track larval abundance, I created an index of abundance using an additive linear model. This method allowed me to account for spatial and temporal variation in sampling both within and between the two sampling programs. Using the constructed larval index as well as the juvenile abundance developed for the most recent stock assessment (SEDAR 2015), I constructed an index of early life survival. Finally, I fit a linearized Ricker model with environmental variables to the idex of survival. Next, in my second research chapter, I looked deeper into where larvae were detected in space to 1) gain information on spawning and dispersal and 2) determine if these spatial patterns were consistent in time. In this chapter, I examined frequency distributions of observed sizes and implemented several spatial models designed to account for the inherent spatial dependency of the data.

Chapter 2: Trends in Relative Abundance and Early Life Survival of Atlantic Menhaden during 1977-2013 from Long-Term Ichthyoplankton Programs

Abstract

Atlantic Menhaden *Brevoortia tyrannus*, a commercially important clupeid, supports one of the oldest and largest commercial fisheries on the US East Coast. Despite recent increases in adult biomass, juvenile indices have declined coast-wide and have remained particularly low in the Chesapeake Bay. In order to understand the underlying causes of this decline, knowledge of larval recruitment is essential. We used larval data collected from two large-scale Northeast Fisheries Science Center ichthyoplankton programs during 1977-1987 and 1999-2013 that occurred from Nova Scotia, Canada, to Cape Hatteras, North Carolina, USA to develop an index of larval abundance. We standardized the larval abundance data to a day-0 age by applying an age-length key from a larval ingression study in the Chesapeake Bay and used a general linear model to account for spatial and temporal changes in sampling. We found larval Atlantic Menhaden abundance increased from 1977-2013, was highest in the winter, and that most individuals were detected at near-shore stations. Over our time series, we also found larval abundance to correspond closely to adult spawning stock biomass. Due to a lack of a direct relationship between our larval estimates of abundance and coast-wide juvenile index, we examined several environmental factors (temperature, Chesapeake Bay discharge, Atlantic Multidecadal Oscillation (AMO), wind speed, and wind direction) that could have an effect on relative larval survival. Larval abundance had a significant negative effect on relative survival. AMO, coastal temperatures, and wind speed also seem to have an effect on early life survival of Atlantic Menhaden, with cooler

temperatures, intermediate wind speeds and negative phase AMO being most favorable for survival. From our findings, it is clear the observed reduction in recruitment is not a problem of larval supply but rather early life survival between the larval and the juvenile stages.

Introduction

Atlantic Menhaden *Brevoortia tyrannus* are an abundant, schooling forage fish that play an important ecological and economic role in coastal and estuarine systems (Vaughan and Smith 1988, Friedland et al. 1989). They are prey for a network of predators in the coastal ocean and estuaries and facilitate upward flux of energy through the food web (Ahrenholz 1991, Annis et al. 2011). Adult Atlantic Menhaden are a migratory, coastal-spawning species, which move seasonally along the North American Coast from Nova Scotia to Florida (Reinjes 1969). The bulk of spawning is traditionally believed to occur in the coastal ocean, peaking during the winter off Cape Hatteras, North Carolina (Ahrenholz et al. 1987). However, some spawning likely takes place throughout the species' range during most of the year (Nelson et al. 1977). Larvae hatch in the coastal oceans and are transported into estuaries where they continue to grow and metamorphose into juveniles (Ahrenholz 1991). Early studies estimated the Chesapeake Bay contribution of juveniles to the spawning stock was 68.8 % (Ahrenholz et al. 1989, ASMFC 2004). While still the primary nursery habitat, contributing proportionally more than other estuaries, recent research has suggested a decline in contribution to the age-1 stock by between 16 and 65% (Anstead and Jones 2014).

The Atlantic Menhaden population has experienced considerable fluctuations in both fishing mortality and biomass (Figure 2.1, SEDAR 2015). While once a coast-wide

reduction fishery, fishing effort has been concentrated in Chesapeake Bay and offshore of New Jersey for the past decade. Even with such a reduction in the spatial range of processing, Atlantic Menhaden continue to support the largest fishery (by volume) on the U.S. Atlantic coast (SEDAR 2015). Biomass estimates are fairly constant through the 1970s and 1980s, but the stock reached an all-time low in biomass in the mid-1990s (Figure 2.1b, SEDAR 2015). The fishery shrank dramatically during this period, with commercial landings decreasing from 401,200 mt in 1990 to 171,200 mt in 1999 (SEDAR 2015). Similarly, juvenile survey trends were high in the 1970s and 1980s, but the estimates declined coast-wide in the 1990s and have remained relatively stable during the 2000s despite estimated increases in abundance and biomass of the adult stock from 2000-2013 (Figure 2.1c). Because of low recruitment of age-0 individuals in the Maryland seine survey since the 1990s, concern has arisen about the state of recruitment to the Chesapeake Bay, Atlantic Menhaden's most productive nursery area (ASMFC 2010). Simultaneously, age-0 surveys north of the Chesapeake Bay have shown increasing values (SEDAR 2015).

Potential causes for changes in recruitment can be classified by the impacted life stage (Houde et al. 2011). First, declines in the adult population, through overfishing or predation, could decrease spawning biomass and resulting recruitment (Houde et al. 2011). Second, eggs and larval Atlantic Menhaden could be experiencing unfavorable oceanic conditions leading to increased early life mortality (Peck et al. 2012, Houde et al. 2011) or reduced success in being transported to appropriate nursery habitats (Houde et al. 2011, Pineda et al. 2007). Finally, juveniles may be exposed to unfavorable nursery conditions, like increased predation or poor water quality, causing increased juvenile

mortality and decreased recruitment (Houde et al. 2011). In this study, we focus on trends in larval abundance and factors that may affect early life mortality.

A combination of factors likely affect larval abundance and early life mortality. Temperature influences timing of spawning (Stegmann and Yoder 1996; Stegmann et al. 1999). Transport (Epifanio and Garvine 2001), development (Nelson et al. 1977), and temperature may be important factors for early life survival (Lewis 1965, Ferraro 1980) of Atlantic Menhaden. Hydrodynamic conditions can affect early life survival because Atlantic Menhaden larvae must be transported into estuarine nursery habitats (Ahrenholz 1991). Larval estuarine ingress is thought to be driven by larval behavior in response to a variety of environmental, tidal, and diurnal cues (Hare et al. 2005, Houde et al. 2009). Additionally, increased freshwater flow events from the Chesapeake Bay may influence nursery habitat quality (Houde et al. 2009), as well as larval transport from the Atlantic Coast near the Chesapeake Bay southwards (Quinlan et al. 1999). This could affect both the timing and location of ingress.

More broadly, large-scale climate variables could be the greatest drivers of recruitment, as they often have an effect on several of the previously mentioned environmental variables. Rice et al. (1999) found that variation in ingress patterns in North Carolina estuaries was driven more by large, climate-scale patterns affecting hydrodynamic conditions rather than localized variation in spawning. The spatial distribution of larval Atlantic Menhaden has not changed significantly when 1977 – 1988 was compared to 1999 – 2008 (Walsh et al. 2015), suggesting adult spawning habitats have not changed. The Atlantic Multidecadal Oscillation (AMO) is a measure of large-scale climate variability and is correlated with Chesapeake Bay recruitment of Atlantic

Menhaden (Wood and Austin 2009). Differences in circulation patterns on a multidecadal scale could affect the transport of eggs and larvae to estuarine habitats. Additionally, AMO phase is correlated with rainfall in most of North America (Enfield et al. 2001) and could have an effect on Atlantic Menhaden recruitment in a way similar to freshwater flow.

The objectives of this study were to examine trends in Atlantic Menhaden larval abundance over time and determine factors affecting survival from larvae to juvenile life stages. We constructed a larval index of abundance from long-term ichthyoplankton programs (1977-1987, 1999-2013), which we compared to juvenile and adult abundance indices from the most recent stock assessment. Finally, we estimated relative survival between larval and age-0 juvenile stages and tested for environmental effects on relative survival between these life stages.

Methods

Larval data

Larval data were obtained from two spatially and temporally extensive sampling programs conducted by the National Oceanographic and Atmospheric Administration (NOAA) on the Atlantic coast of the U.S. Data from 1977-1987 were obtained from the Marine Resources Monitoring, Assessment, and Prediction (MARMAP) program and data from 1999-2013 were obtained from the Ecosystem Monitoring (EcoMon) program. Although EcoMon began in 1992, only ichthyoplankton samples since 1999 have been processed. Therefore, we began our analysis of this dataset in 2000, which included the entire spawning season beginning in September 1999. Both surveys sampled the same spatial extent of shelf waters from North Carolina to Nova Scotia on a roughly bi-monthly

basis. MARMAP used primarily a fixed station design (Sibunka and Silverman, 1984) and EcoMon used a stratified random design, with strata determined by depth and latitude (Walsh et al. 2015). Plankton sampling was conducted with a 61 cm bongo net by double oblique tows sampling from the surface to within 5 meters of the bottom to a maximum depth of 200 meters in deeper water, and back to the surface at 1.5 knots. Ichthyoplankton mesh size was 505 µm during MARMAP and 333 µm during EcoMon. Samples were fixed in a 5% formalin solution at sea and larvae were transferred to ethanol during processing. Samples were processed at the Morski Instytut Rybacki in Szczecin, Poland, or the Northeast Fisheries Science Center to determine counts of all species (identified to the lowest taxon) and length measurements. Length was measured for up to 50 individuals for each species per tow; if more than 50 individuals were present, a random subsample of 50 was taken to characterize the length composition.

There were some differences in sampling methods between programs. Environmental data were collected at most of the sampling locations, and sampling techniques and instrumentation varied between MARMAP and EcoMon. During the MARMAP Program, water temperatures were collected with bucket thermometer, water bottle with reversing thermometer, mechanical bathythermograph, or expendable bathythermograph, and salinity with water samples and a salinometer (Holzwarth and Mountain, 1990; Mountain et al., 2004; Sibunka and Silverman, 1984). During the EcoMon program, water temperature and salinity were measured using conductivity, temperature, depth probes (Mountain et al., 2004; Taylor and Bascunan, 2001).

We restricted our analyses to encompass the primary spatial and seasonal occurrence of Atlantic Menhaden larvae on the shelf. Fourteen of the EcoMon programs

shallowest strata, from Southern New England to Cape Hatteras, NC, were used because very few Atlantic Menhaden larvae were observed outside these regions (Figure 2.2). Similarly, surveys conducted in July and August were excluded because no Atlantic Menhaden larvae were observed during July and only 15 larvae were observed during August over the entire study period, while the other months ranged from 1,468 to 304,931 individuals. To capture seasonal spawning dynamics, we treated September as the beginning of the larval year such that larvae that hatched during September-December would be added to those from January through May of the following year. We paired months (Sept-Oct, Nov-Dec, Jan-Feb, Mar-Apr, and May-Jun) to reflect the bimonthly sampling design.

Index of Larval Abundance

Prior to constructing our index of larval abundance, we corrected for differences in mesh size selectivity among programs. The mesh size of the bongo net has a significant effect on selectivity (Johnson and Morse 1994). This effect was largest in fish below 3 mm, where the 333 μm mesh caught four times as many fish as the 505 μm. In order to account for this change in gear, we calculated correction factors for each 1 mm size bin below 9 mm (Table 2.1) from the data presented in Johnson and Morse (1994). After applying this correction to the raw counts, we recalculated abundance at age and overall abundance for all Atlantic Menhaden caught in the MARMAP program.

We also corrected for variation in age of larvae caught throughout the sampling season in order to estimate a standardized measure of larval production (see Richardson et al. 2010 for a more in depth explanation). Mean length at daily age (from Lozano et al. 2012) was used to estimate the ages of all measured larvae, interpolating ages linearly

between means. We assumed a constant mortality rate of 0.179 d-1 (for clupeid species; Houde and Zastrow 1993) and then used this mortality rate to construct an estimate of 0-day-old abundance. This information was then used to further correct larval abundance per tow. We performed a sensitivity analysis, using a daily mortality of one half the literature value at 0.09 d-1, and observed no differences in the trends of the abundance index.

To correct for variation in sampling location and timing, we used a log-linear model to construct a larval index of abundance for Atlantic Menhaden (Maunder and Punt 2004). By log transforming a dependent variable, we were better able to satisfy the assumption of normality. Log catch per tow was modeled as a linear function of year, month, and stratum,

$$Log_e(A + 0.6) = \mu + M + Y + S + \varepsilon \qquad (2.1)$$

where A is the abundance for each tow, adjusted for mortality by larval length, μ is the intercept of the model, M is month, Y is year, S is stratum, and ε is a normally distributed error term. We included a constant of 0.6, approximately half of the lowest positive value of A, in the model to prevent taking the logarithm of 0. Sensitivity analyses with constants 0.3 and 1.2 produced approximately the same results for the trend in the index of abundance over time. Due to the unbalanced design of the sampling programs, we used a Kenward-Roger approximation (Kenward and Roger 1997) to calculate adjusted degrees of freedom to estimate standard errors and confidence intervals.

Survival Index

To estimate if survival changed over time and to test whether early life survival was related to a suite of environmental factors, we constructed an index of survival from our larval index and the young-of-the-year (YOY) index from the most recent Atlantic

Menhaden stock assessment (SEDAR 2015). The YOY index was generated using a hierarchical model that combined sixteen fishery-independent YOY data sets from New England to Georgia into a single index (Conn 2010, SEDAR 2015).

The survival index was calculated as the logarithm of the YOY index divided by the larval index,

$$I_S = \log\left(\frac{I_J}{I_L}\right), \tag{2.2}$$

where IS, IJ, and IL are the early life survival index, the YOY juvenile index, and the larval index, respectively. This index follows the traditional form used in many stock-recruitment analyses that incorporate additional explanatory variables (Quinn and Deriso 1999).

We obtained climate data (AMO, wind, freshwater flow, and temperature, Table 2.2) for inclusion as covariates in our survival model. We used information from the same period (September through June) for AMO, freshwater flow, and coastal temperature. However, we only used wind information from November through March, the critical part of the year when late-stage larvae ingress into Chesapeake Bay (Lozano et al. 2012). Similarly, we used Chesapeake Bay temperature information from November to April in order to include the entire window of time from surviving ingress to when the bulk of the youngest fish metamorphose into juveniles. Although surface temperature measurements were only from the Patuxent River, temperature in the major tributaries and the main stem of Chesapeake Bay are highly correlated (Humphrey pers. comm. 2015).

All environmental variables were summarized into annual indices by calculating the arithmetic mean except the coastal water temperature. These data were obtained from surface water temperature measurements collected on MARMAP and EcoMon cruises.

However, not all cruises had temperature data available for each sampling event, particularly during the earlier time series. For this reason, annual average temperature was constructed using a linear model with month, season, and sampling strata as categorical variables,

$$T_C = \mu + M + Y + S + \varepsilon. \quad (2.3)$$

where, Tc is coastal temperature, μ is the intercept of the model, M, Y, and S correspond the month, year, and stratum, and ε is a normally distributed error term.

We used a linear model to examine the relationship between survival and several environmental variables,

$$I_S = \mu + I_L + AMO + T_B + T_c + F + W_D + W_S + \varepsilon, \quad (2.4)$$

where μ is the intercept, IL is the larval index, AMO is the calculated AMO index, TB and TC are the bay and coastal temperature indices, respectively, F is the mean freshwater flow from the Chesapeake Bay from September-June, WD and WS are the indices for wind speed and direction from the Norfolk International Airport, respectively, and ε is a normally distributed error term. This procedure, using a linearized Ricker model, modified to include environmental variables is a commonly used technique to evaluate potential environmental effects on spawning success by comparing recruits to survivors (Prager and MacCall 1993, Jacobson and MacCall 1995). We conducted a linear regression of all model subsets in R and performed an AICc (Akaike Information Criterion with a correction) comparison to select the best model of larval survival. We used the AICc due to the relatively low number of observations compared to the number of estimated parameters (Burnham and Anderson 2002). We tested for significance ($\alpha = 0.05$) of the effects of the environmental factors on survival in our best fit models.

Results

The relative abundance of larval Atlantic Menhaden increased over time (Figure 2.3). The lowest observed larval abundance estimate occurred in 1988, and the peak larval abundance estimate occurred in 2008. Index values remained relatively constant and low during 1977-1988. Beginning in 2000, Atlantic Menhaden larval abundance increased substantially, on average, by 35% each year, compared to an average change of -0.18% between 1977 and 1988. Further, the ten highest abundance estimates all occurred during the most recent (EcoMon) program. The four remaining years from that same survey (2000, 2001, 2003, and 2005) were comparable to larval abundance estimates from the earlier MARMAP program.

Peak larval abundance occurred during November-December, which was more than five times higher than the second highest month pairing on average (Figure 2.4a). Larval abundance was lowest in the north, with highest observations in shallow strata off of the North Carolina coast (Figure 2.4b). Additionally, larval abundance was higher in shallow, near-shore strata when compared to deep water strata of similar latitude.

Relative survival decreased fourfold during 1977-2013 (Figure 2.5a). The survival index was negatively correlated with the larval abundance index (coef=-2.68; Table 2.3, $p<0.001$; Figure 2.5b). Including environmental variables resulted in improved AICc scores over models that did not include them (Table 2.3). The best ten models had similar AICc scores, with values from 1.99-4.71, which were all greater than 2 AICc units lower than the null model (AICc = 6.69). Wind speed and coastal temperature were both included in six out of the 10 best performing models. AMO was included five times, bay temperature included three times, and wind direction twice. In these top models, the

negative effect of AMO was significant ($p<0.05$) in four of the five models where it was included (Table 2.3, Figure 2.6a). Relative survival was negatively related to coastal temperature ($p<0.05$) in two of the six models in which it was included, but not when AMO was also a factor (Table 2.3; Figure 2.6c). Although temperature is a component of AMO, the two variables had a Pearson correlation of 0.19. Wind speed had a significant effect on survival in five of the six models in which it appeared (Table 2.3); the relationship appears to be nonlinear between wind speed and Atlantic Menhaden early life survival, with an optimal survival at speeds averaging between 5 and 6 m/s (Figure 2.6e). Wind speed and AMO were negatively correlated at a factor of -0.79 and were the most correlated of all variables used. Given this level of correlation, we are confident that variance inflation is not an issue in this analysis. Bay temperature, fresh water flow, and wind direction were not found to have a significant effect on survival (Table 2.3, Figure 2.6b, d, f).

Discussion

Larval Atlantic Menhaden abundance increased substantially since the late 1970s. The observed increase in our larval index is comparable with the recent increase in population fecundity (i.e., estimated egg production) from the 2015 Atlantic Menhaden stock assessment (SEDAR 2015). The stock assessment estimates of population fecundity approximately doubled between 2000-2003 and 2009-2013, similar to our index of larval abundance. We did not observe the same pattern of interannual variability during the 1980s in our larval abundance index as was present in the estimates from the stock assessment. However, the fishery independent data on adults included in the assessment only extended as far back as 1988. So, it is not surprising the short time-scale variability

does not match up well in the early period. Even still, the high index in the most recent period is a positive sign for Atlantic Menhaden populations, and both larval index and population fecundity appear to have been on the rise in the past decade. This corresponds with the sustained low estimated fishing mortality since 2000 (Figure 2.1a, SEDAR 2015).

Comparing our analysis to the age 1+ biomass estimated in the most recent stock assessment (SEDAR 2015) revealed a relationship between our larval index of abundance and the adult spawning stock, particularly for our most recent sampling program (Figure 2.7), and the pattern was strongest for the period after 1999. We have greater confidence in this later period due to the reduction in mesh size, which in turn, increased the probability of detecting the smallest larvae, particularly below 9 mm and with decreasing effects at larger sizes. Additionally, the stock assessment only has adult fishery-independent data available since 1988, and so the adult biomass estimates may be less reliable before 1988. Further, although we included a correction for the change in gear between surveys, it is possible that we are still underestimating Atlantic Menhaden larval abundance from the earlier MARMAP program due to a reduced ability to detect the smallest (<10 mm) larva. Even still, these results strongly suggest the coast-wide reduction in juvenile abundance does not appear to be a problem of larval supply.

The seasonal and spatial patterns observed in the larval abundance data generally agree with the previously described pattern of spawning of Atlantic Menhaden. Peak spawning occurred in the winter, off the coast of Cape Hatteras, North Carolina (Dryfoos et al. 1973; Nicholson 1978). Larval abundance was more than five times higher in November-December than any other time of the year. Similarly, we observed highest

larval abundance, on average, off the coast of North Carolina. However, shallow strata all along the Atlantic Coast had comparable abundance estimates with average means between 58% and 38% of what was observed near North Carolina. Spawning in these more northern strata takes place on the adults north to south migration that begins in the late summer (Judy and Lewis 1983; Ahrenholz 1991; Berrien and Sibunka 1999). In addition, our results of higher abundances in shallow strata correspond with previous modeling research (Stegmann et al. 1999).

Our study excludes some shallow water habitat and the southern-most portion of the Atlantic Menhaden's spatial range, but we think that the results should still be fairly robust. It has been documented that some spawning occurs within the Narragansett Bay (Keller et al. 1999). However, based on the general observed trend of increasing larval abundance southward (Figure 2.4b), coupled with the generally accepted theory of migratory spawning behavior increasing southwards (Ahrenholz 1991), we are assuming larvae occurring in these northern estuaries to be negligible compared to the scope of the study. The accepted view of Atlantic Menhaden migratory dynamics includes an age-based stratification along the Atlantic Coast with the population south of North Carolina to be made up mostly of age-0 and age-1 individuals (Nicholson 1978). Based on this assumption, the majority of the spawning stock biomass would exist within the range of our surveys. However, further research into the age distribution of Atlantic Menhaden, particularly in the southern portion of the range would be valuable. Further, Quinlan et al. (1999) found that, due to the hydrological conditions, it is unlikely that larvae spawned south of Cape Hatteras, NC could be transported north to nursery areas such as the Chesapeake and Delaware Bays. The majority of the surveys included in the juvenile

index are from North Carolina and northward, larval supply to these estuaries north of Cape Hatteras is hypothesized to occur primarily from spawning north of the estuary, and larvae are transported by southwestward along-shelf currents to the estuary (Stegmann et al. 1999; Quinlan et al. 1999).

Although the data used in this analysis were collected in two programs that used slightly different techniques, we do not believe that this affected the outcome of our work. The primary differences between the two programs were minor variations in sampling frequency, as well as a change in mesh size from 505 to 333 μm. We accounted for sampling changes by including month as a factor in our linear model. We accounted for the change in mesh size by applying a selectivity correction to the MARMAP data using the results of Johnson and Morse (1994), who performed a gear comparison test for the exact survey included in our analyses. Although the data from the MARMAP period were lower on average than those from the ECOMON sampling, larval abundance values from the beginning of the EcoMon period (early 2000s) are similar to those from the MARMAP survey and agree with the changes estimated in the stock assessment.

We estimated a substantial decline in survival over time (Figure 2.5a). At least part of this decline in survival with the increase in larval supply could be explained by density dependence (Figure 2.5b). During the EcoMon period, we found higher larval abundance than during the MARMAP program (Figure 2.3). However, the average juvenile abundance (Figure 2.1c, SEDAR 2015) showed the reverse trend. Our survival index is simply the ratio of these two indices. Thus, declining survival is expected. Density dependence has been proposed to have a role in Atlantic Menhaden populations before (e.g. Schaaf and Huntsman 1972, Nelson et al. 1977, Reish et al. 1985). Two

possible underlying mechanisms included predation on eggs and larvae by adults (Nelson et al. 1977) and decreased growth prior to recruitment due to limited resources (Reish et al. 1985). If density dependent growth does have an effect on Atlantic Menhaden survival, this effect would become greater in years with warmer average temperatures (i.e. during the EcoMon program) due to increased metabolic demands and higher rates of starvation (Houde 1989).

We expected to see a relationship between Atlantic Menhaden survival and AMO based on previous work on fish populations in the Chesapeake Bay (Wood and Austin 2009). Wood and Austin (2009) found decadal-scale variability, similar to the AMO, accounted for the majority of variance of fish abundance. The most likely mechanism proposed for such a relationship was the impact of broad scale environmental factors impacting shelf spawning species such as Atlantic Menhaden at multiple life stages. Such broad patterns would be difficult to detect using any one environmental factor. They also found evidence supporting a significant regime shift in 1992, negatively affecting coastal spawning species, such as Atlantic Menhaden. The AMO phase was negative in the 1980s and 90s and has moved into a positive phase since the late 1990s (Nye et al. 2013). Our results support the importance of decadal scale variation, though not a major regime shift in the early 1990s as suggested by Wood and Austin (2009). Overall, we detected a negative relationship between AMO and survival (Figure 2.6a). If this is an important factor driving Atlantic Menhaden survival, then it is possible some of the observed decline is part of a naturally occurring cycle; however, our data do not span an entire AMO cycle.

However, it is possible that AMO may not be affecting Atlantic Menhaden

equally over their entire range. Specifically, juvenile survival has been found to be inversely correlated with AMO in Chesapeake Bay, but positively correlated in Southern New England estuaries (Buchheister et al. 2015). Therefore, if we were to focus solely on Chesapeake Bay recruits, instead of the entire juvenile index, we may have found an ever stronger negative relationship between survival and AMO.

Survival was not significantly related to Chesapeake Bay temperature, but this could be due to only using spatially limited temperature data (from Chesapeake Bay only). Although, mean winter to spring water temperatures of the five major estuaries (Chesapeake Bay, Delaware Bay, Long Island Sound, Narragansett Bay, and Buzzards Bay) of the Northeast U.S. Coast are fairly correlated (Bell et al. 2014). Still, to describe the effect of temperature in the juvenile habitat, it may be necessary to incorporate measurements from most of the large important nursery areas, such as the Delaware Bay (Light and Able 2003) and Albemarle Sound (Stegmann et al. 1999). However, even with such information we would need to make some strong assumptions about the relative importance of nursery habitats across such a large timeframe. Alternatively, temperature may not have a detectable effect, possibly due to trade-offs between increased growth rates with warmer spring temperatures and lower survival as temperatures increase and food availability declines (Deegan 1990).

Winds speed could affect early life survival through multiple mechanisms such as feeding and transport. Due to the planktonic nature of Atlantic Menhaden larvae, particularly young larvae, early transport is predominately driven by physical factors such as wind-driven Ekman transport (Epifanio and Garvine 2001). Of course, the directionality of wind is also important, depending on the depth at which larvae are

occurring. For example, up-estuary wind would favor surface oriented larvae. However, Atlantic Menhaden larvae ingressing into the Delaware Bay have been found to be distributed evenly among depths (Schieler et al. 2014). We expected wind speed to have a negative effect on survival at particularly high and low levels, as some wind mixing could increase larval prey occurrence, but too much turbulence could do the opposite (Maillet and Checkley 1991). Our results suggest there may be an optimum range of wind speed for Atlantic Menhaden survival, although more work in this area is needed because we had relatively few observations with high average wind speed. This finding is reminiscent of the theory of an optimal environmental window (Cury and Roy 1989) which shows that pelagic fish have best reproductive success in upwelling environments when the wind speeds are at intermediate levels to maximize larval predation success. Additionally, we only considered linear relationships for environmental variables, so a non-linear relationship where intermediate values are more favorable than both high and low values, does not match the assumptions of the survival model used.

We found no evidence of an effect of wind direction on larval Atlantic Menhaden survival. Successful ingress of Atlantic Menhaden larvae is a complex process that requires transport of larvae to estuary mouths, which is thought to be primarily north of estuaries on the northeast U.S. coast (Stegmann et al. 1999, Quinlan et al. 1999), and up estuary transport to juvenile habitats via residual bottom water inflow and wind forcing (Hare et al. 2005). We expected winds coming from the northeast to be most ideal for successful ingression into the Chesapeake Bay, thus increasing survival, because northeast winds produce significant residual inflow on the northern (where potential source of larvae occurs) side of the inlet (Valle-Levinson et al. 2001). However, wind

direction was fairly consistent across years, coming from the northwest, the direction that is most efficient at flushing water out of the bay (Valle-Levinson et al. 2001). What variation we did observe did not appear to affect survival. Schieler et al. (2014) also found no relationship between Atlantic Menhaden ingress into Delaware Bay and along-shelf or along-estuary winds.

Freshwater flow had no significant effect on Atlantic Menhaden survival. We expected years with higher mean freshwater to promote ingress. Higher freshwater flow could mean greater transport ingress via increased residual bottom water inflow (Hare et al. 2005). Additionally, greater freshwater flow may increase prey, particularly copepod, abundance (Houde et al. 2009). However, there was no evidence of a relationship between flow and Atlantic Menhaden survival. This may be due to the length and coverage of our time series, as any environmental variables with weak to moderate effects would be difficult to detect in this type of analysis due the many potential sources of variation.

Atlantic Menhaden is one the most abundant forage fish species on the Atlantic coast and transfers substantial amounts of energy through the food web. The most recent assessment reported a healthy population with high abundance and no overfishing in recent years. Our analysis of two large-scale ichthyoplankton surveys indicated that the Atlantic Menhaden larval population increased substantially in the last decade, which corresponds well with the most recent stock assessment estimates of spawning stock biomass. Pre-recruit survival, however, appears to have decreased substantially in recent years, which may be driven by density dependence. Additionally, AMO, coastal temperature, and wind speed all appear to have effects on larval survival.

Tables and Figures

Table 2.1. Correction factors used for larval Atlantic Menhaden caught in the MARMAP ichthyoplankton survey (1977-1987) for comparison with individuals caught in the EcoMon ichthyoplankton survey (2000-2013) calculated from Johnson and Morse (1994).

Length Bin (mm)	Correction Factor
< 3	4.033
3-4	1.748
4-5	1.402
5-6	1.576
6-7	1.255
7-8	1.330
8-9	1.328

Table 2.2. Environmental data included in a model examining the early life survival of Atlantic Menhaden.

Data	**Units**	**Location of Collection**	**Source**	**Month Range**
AMO	NA	NA	NOAA	Sep-Jun
Wind Speed	m/s	Newport, VA	NOAA	Nov-Mar
Wind Direction	degrees	Newport, VA	NOAA	Nov-Mar
Freshwater Flow	ft^3/sec	Chesapeake Bay Mouth	USGS	Sep-Jun
Chesapeake Bay Temperature	°C	Solomons, MD	CBL	Nov-Apr
Coastal Temperature	°C	NA	EcoMon/ MARMAP Surveys	Sep-Jun

Table 2.3. AICc (Akaike Information Criterion with a correction) results and model coefficients from null survival model and top 10 scoring models by AICc of a linear model of Atlantic Menhaden survival. Variable names are as follows: larv- larval index of abundance, AMO - Atlantic Multidecadal Oscillation, b_temp - Mean Chesapeake Bay winter/spring temperature collected from the Patuxent River, c_temp - average coastal temperature derived from measurements taken during MARMAP and EcoMon ichthyoplankton surveys, flow – mean freshwater flow from the Chesapeake Bay mouth, w_spd - wind speed collected from Norfolk, VA international airport, w_dir - wind direction collected from Norfolk, VA international airport. Asterisk indicates a significant parameter ($p<0.05$).

Model	larv	AMO	b_temp	c_temp	flow	wind_spd	wind_dir	AICc
Null Model + AMO + c_temp	-1.96*	-1.96*	-	-0.131	-	-	-	1.99
Null Model + c_temp + w_spd	-1.99*	-	-	-0.165*	-	0.718*	-	2.04
Null Model + AMO	-2.18*	-2.21*	-	-	-	-	-	2.37
Null Model + c_temp + w_spd + w_dir	-2.20*	-	-	-0.196*	-	0.685*	-0.00612	3.10
Null Model + AMO + b_temp	-1.83*	-1.89*	-0.174	-	-	-	-	3.68
Null Model + w_spd	-2.38*	-	-	-	-	0.608*	-	4.19
Null Model +AMO + c _temp + w_spd	-1.92*	-1.12	-	-0.149	-	0.405	-	4.25
Null Model + AMO + c_temp + w_dir	-2.13*	-1.79*	-	-0.155	-	-	-0.00448	4.29
Null Model + b_temp + c_temp + w_spd	-1.80*	-	-0.112	-0.140	-	0.683*	-	4.59
Null Model + b_temp + w_spd	-1.84*	-	-0.234	-	-	0.608*	-	4.71
Null Model	-2.68*	-	-	-	-	-	-	6.69

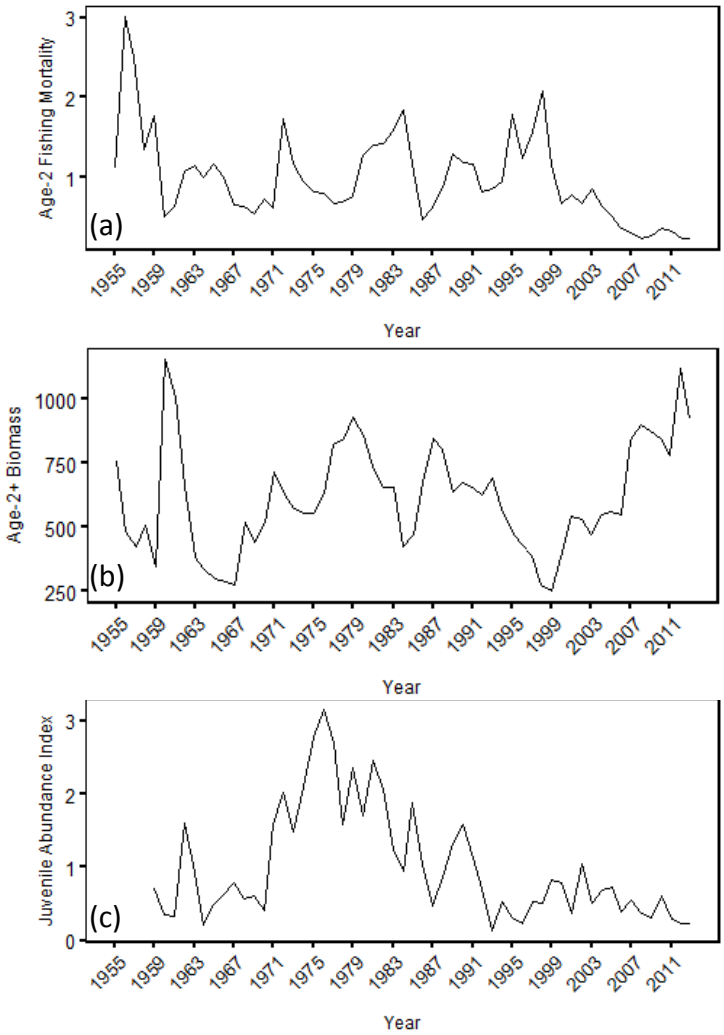

Figure 2.1. Fishing mortality, total biomass, and juvenile abundance obtained from SEDAR (2015). (a) Age-2 fishing mortality was chosen as it is the most highly selected age. (b) Predicted biomass (1000s mt) of age-2 + individuals. (c) Scaled juvenile index of abundance as calculated using surveys from New England to Georgia.

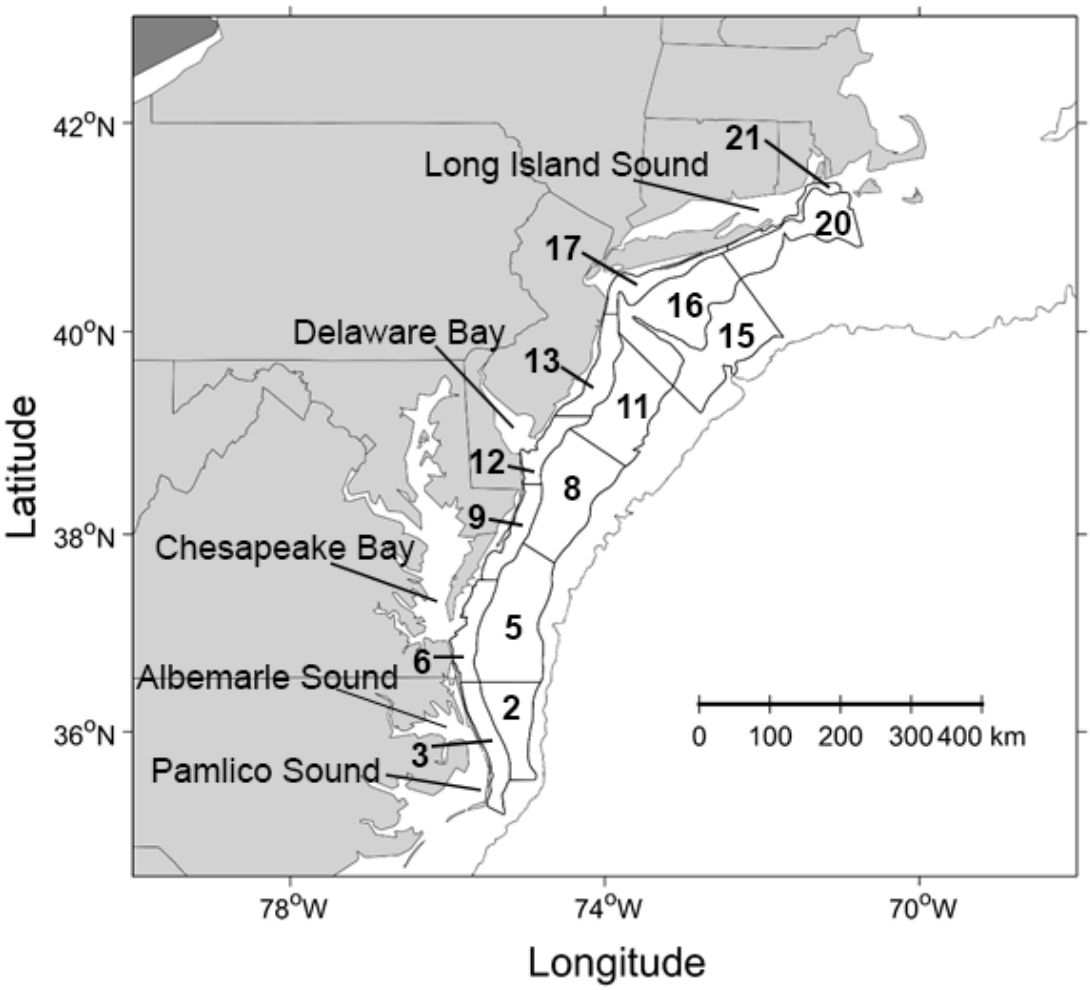

Figure 2.2. Map of strata used in MARMAP (1977-1987) and EcoMon (1992-present) sampling programs conducted on the Atlantic Coast of North America from Nova Scotia, Canada to North Carolina, USA. Sampling strata are labeled by their corresponding EcoMon stratum number. Bays are labelled but were not sampled.

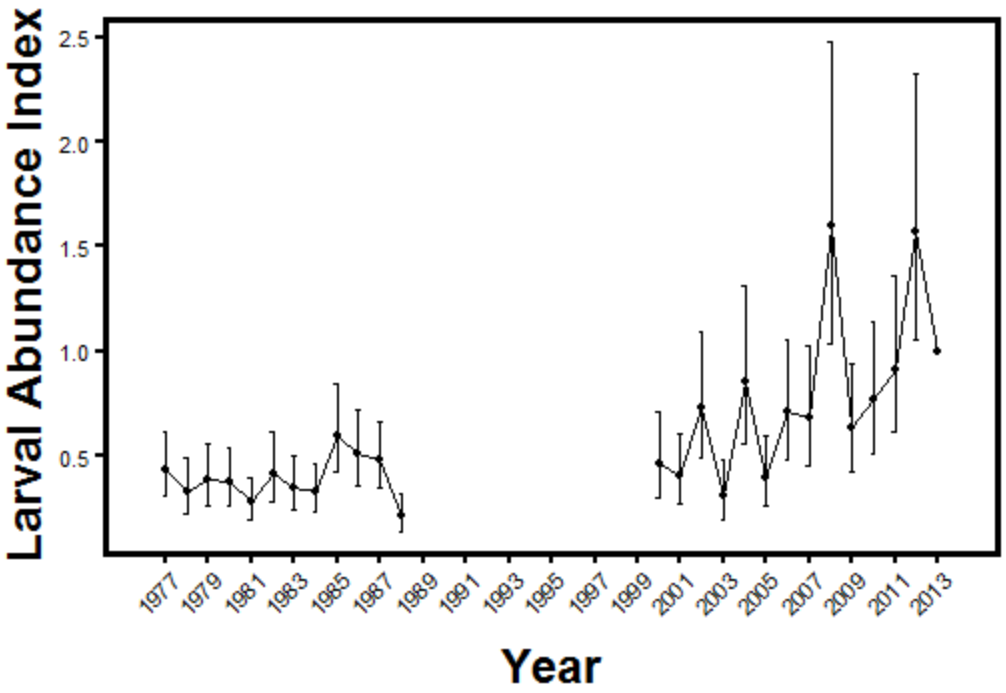

Figure 2.3. Atlantic Menhaden larval abundance index (relative effect sizes from a linear model estimating relative larval abundance) constructed from MARMAP (1977-1987) and EcoMon (2000-2013) ichthyoplankton surveys on the Atlantic coast from southern New England to Cape Hatteras, NC (strata shown in Figure 2.2). Error bars represent 95% confidence intervals calculated using the Kenward-Roger procedure.

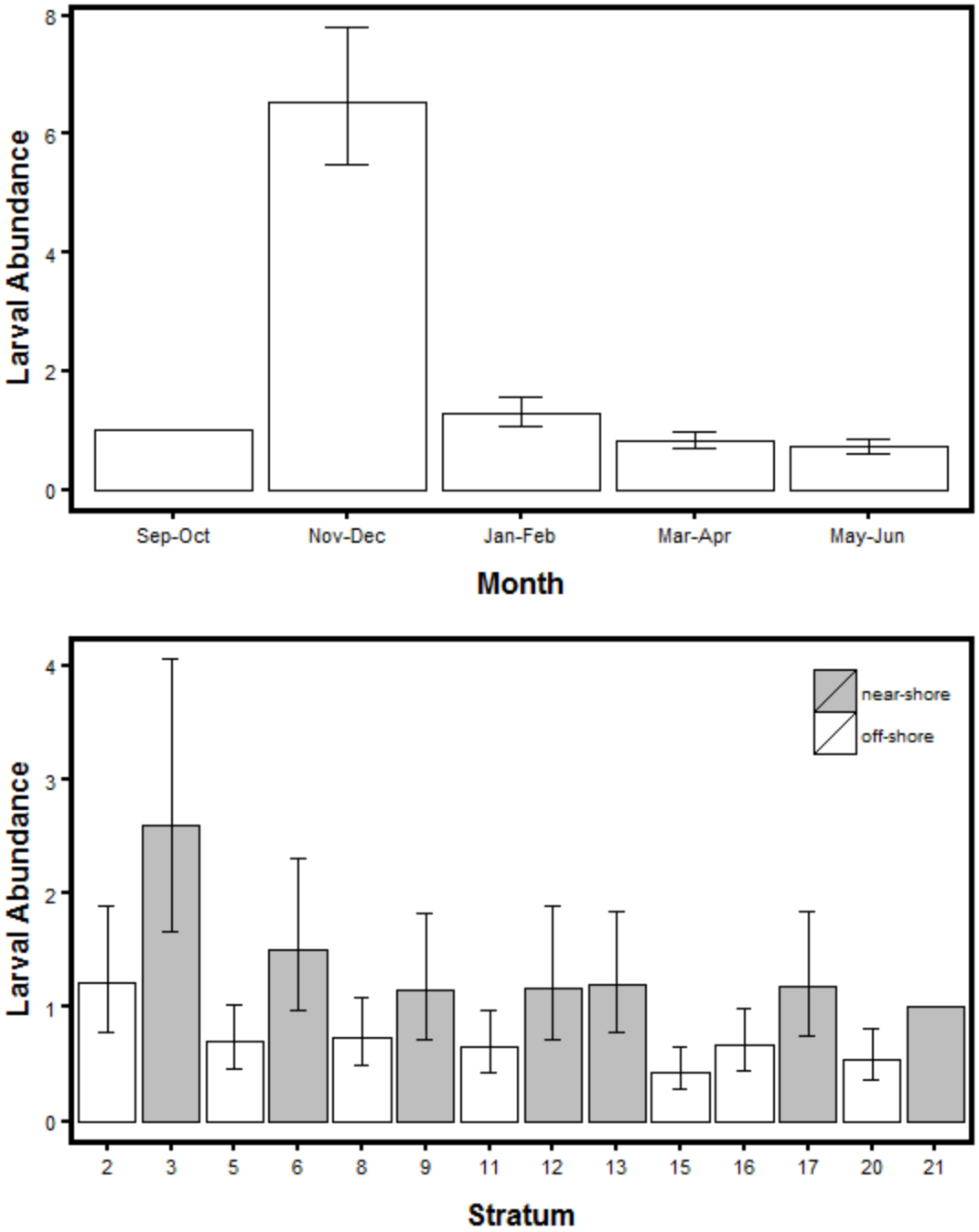

Figure 2.4. Month (a) and stratum (b) relative effect sizes on the arithmetic scale from a linear model estimating relative Atlantic Menhaden larval abundance from MARMAP (1977-1987) and EcoMon (2000-2013) ichthyoplankton surveys on the Atlantic coast from southern New England to Cape Hatteras, NC. Error bars represent 95% confidence intervals calculated using the Kenward-Roger procedure. We could not calculate confidence intervals for Sep-Oct and stratum 21 as these levels were used to estimate all other levels. See Figure 2.1 for strata locations.

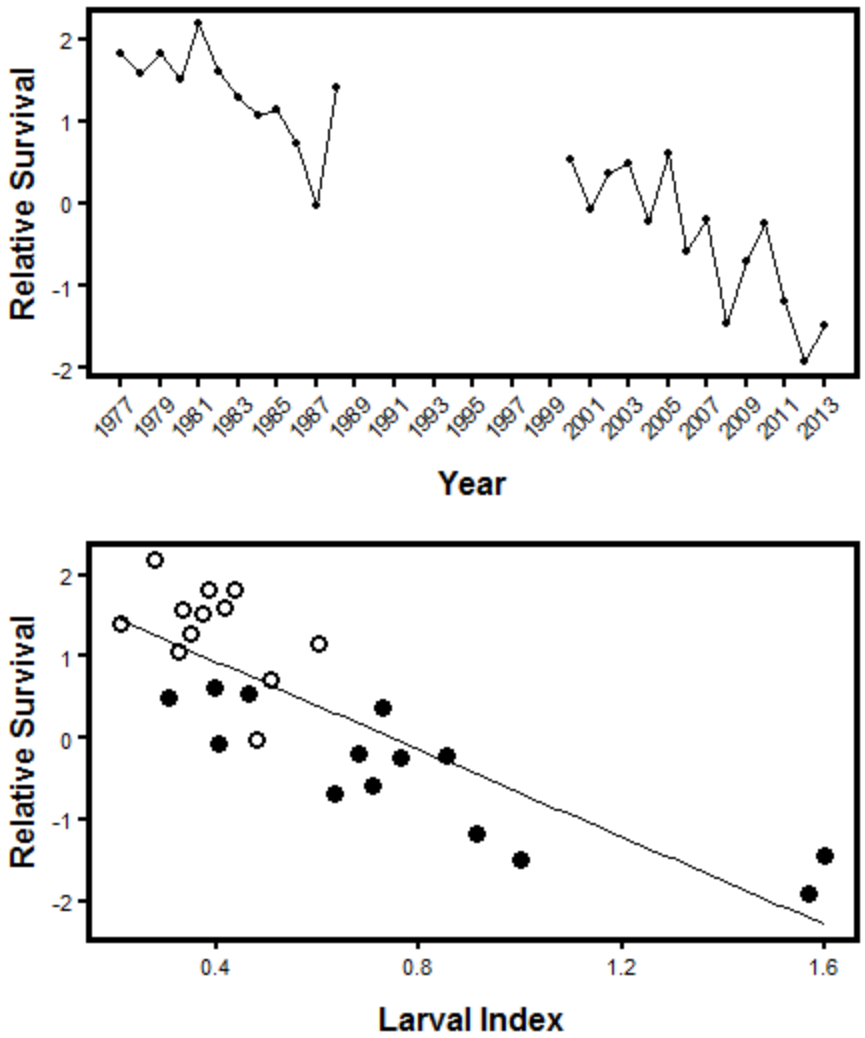

Figure 2.5. (a) Relative early life survival, calculated as the natural log of the juvenile index (from the 2015 stock assessment) over the larval index (calculated using a linear model) by year. (b) Linear regression showing the relationship between relative survival and relative larval abundance for Atlantic Menhaden from MARMAP (1977-1987; hollow points) and EcoMon (2000-2013; solid points) ichthyoplankton surveys on the Atlantic coast from southern New England to Cape Hatteras, NC ($p<0.001$).

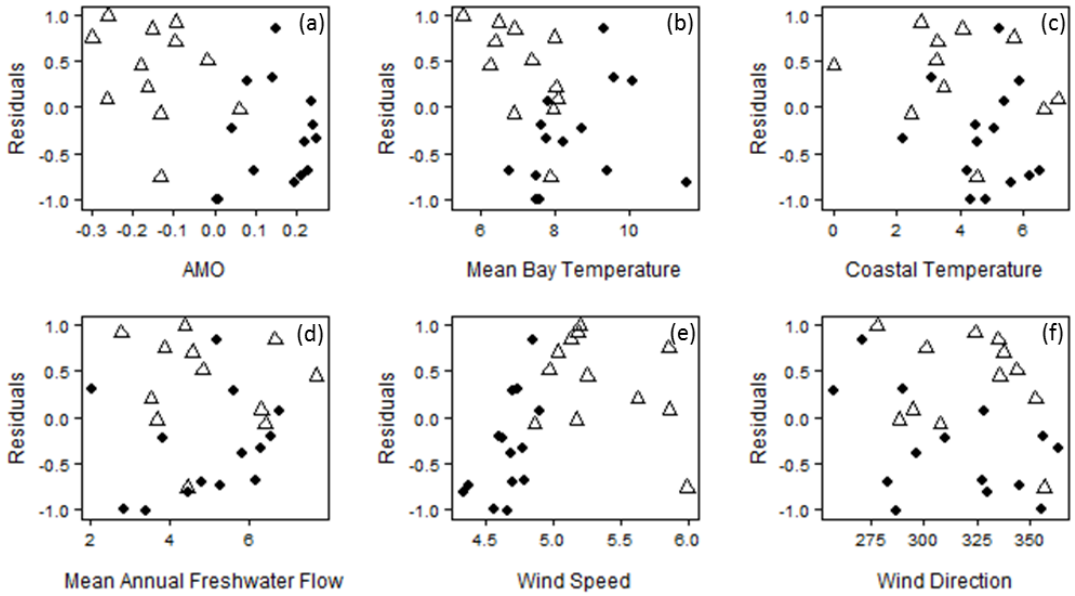

Figure 2.6. Residuals from a linear survival model plotted against six environmental variables. (a) AMO (Atlantic Multidecadal Oscillation) averaged over Sep-Jun. (b) Mean Chesapeake Bay temperatures (°C) Nov-Apr taken from the Patuxent River. (c) Coastal temperatures (°C) modeled from MARMAP (1977-1987; open triangles) and EcoMon (2000-2013; closed dots) ichthyoplankton surveys on the Atlantic coast from southern New England to Cape Hatteras, NC. (d) Mean freshwater flow (ft^3/sec) from Nov-Mar discharged from the Chesapeake Bay. (e) Mean wind speed (m/s) and (f) direction (degrees from North) detected at the Chesapeake Bay mouth in Newport News, VA.

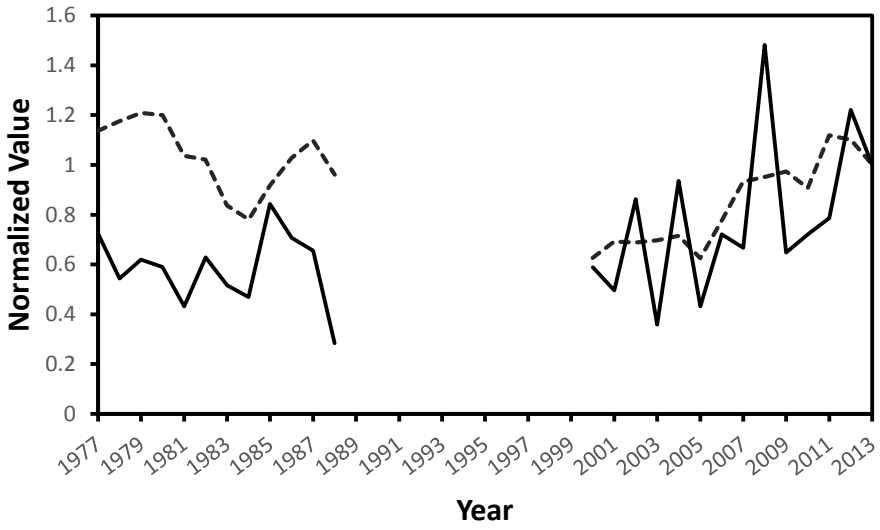

Figure 2.7. Normalized values of age 1+ Atlantic Menhaden estimated biomass (dashed line; SEDAR 2015) plotted with normalized larval abundance index values (solid line) as seen in Figure 2.3.

Chapter 3: Spawning Locations and Larval Dispersal of Atlantic Menhaden during 1977-2013

Abstract

An improved understanding of recruitment dynamics is important for management of fisheries species. Atlantic Menhaden *Brevoortia tyrannus* have particularly complex recruitment dynamics as a migratory, coastal-spawning species, which move seasonally along the North American Coast from Nova Scotia to Florida. Despite a coast-wide reduction in juvenile production, Atlantic Menhaden continues to supports one of the oldest and largest commercial fisheries on the US east coast. We used a stochastic partial differential equation (SPDE) model to estimate spawning location and larval dispersal on the Atlantic Coast over two time periods, 1977-1987 and 2000-2013 with data from the Northeast Fisheries Science Center ichthyoplankton surveys. Atlantic Menhaden spawning appears to primarily occur near shore over a large spatial range, from southern New England to North Carolina, over the majority of the year, but at greatest levels during November and December. Larger, older larvae, were found over a similar spatial and temporal range, dispersing farther from shore. Between the two periods, we observed an increase in secondary, spring-time spawning events. We observed no major, directional spatial shift in spawning or dispersal. However, there was a substantial change in estimated spawning activity near Delaware Bay. During both periods, spawning and dispersal increase southwards, but overall spatial coverage of both activities varies greatly among years until the mid-2000s, when the Atlantic Menhaden population is believed to have recovered, we observed consistent and large areas of spawning and larval dispersal. For a bet hedging species such as Atlantic Menhaden, the greater the area young are exposed, the greater chance of success for that generation.

Introduction

Recruitment dynamics in marine fisheries are often very complex, due to a dynamic interplay between physical and biological factors (Forgarty et al. 1991). However, an understanding of these dynamics at different spatial and temporal scales would be useful for management. In open marine populations, the local production of offspring may have little direct impact in setting local population size (Caley et al. 1996) because of a combination of complex life history and variation in physical environments. Therefore, knowledge of detailed spatial and temporal variation in early recruitment allows scientists to separate localized from population-scale fluctuations in abundance and examine such changes in relation to physical and biological factors including climate change.

Atlantic Menhaden *Brevoortia tyrannus* is an abundant forage fish species on the Atlantic coast of the United States. Not only are they an important prey species, transferring energy up through the food web (Ahrenholz 1991, Annis et al. 2011), but they are economically valuable and make up one of oldest industrialized fisheries in the United States (Vaughan and Smith 1988, Friedland et al. 1989). Atlantic Menhaden are migratory, coastal-spawners, ranging from Nova Scotia, Canada to Florida, USA (Reinjes 1969). Eggs are released and hatch in the coastal ocean before larvae are transported to nursery habitats (i.e. estuaries) where they metamorphose into juveniles (Ahrenholz 1991). While there was recently concern over the status of the spawning stock currently, the stock is not overfished and is overfishing not occurring (SEDAR 2015).

Although the adult stock appears to be recovered, there have not been substantial changes in coast-wide recruitment since the 1990s (SEDAR 2014). However, recruitment patterns are not consistent across space. While recruitment patterns in nursery habitats in

southern New England are highly correlated with each other, as are patterns in nursery habitats near the Chesapeake Bay, the two regions show inverse patterns (Buccheister et al. 2015). Historical estimates suggest that the Chesapeake Bay contributed as much as 69% of total recruits to the spawning stock (Ahrenholz et al. 1989, ASMFC 2004). Although still proportionally the most important nursery area, more recent research conducted 2009-2011, has suggested a lower, but variable contribution from the Chesapeake Bay between 25 and 59% (Anstead and Jones 2014).

In order to identify the sources of variation in menhaden recruitment, we must look closely at the early life stages of Atlantic Menhaden, beginning with spawning. Menhaden spawning has not been directly observed in nature. Thus, knowledge of spawning behavior has been inferred from planktonic sampling of menhaden eggs and larvae (e.g., Checkley et al. 1999, Hare et al 1999) and ova classification of adult females (e.g. Lewis et al. 1987). It is generally accepted that the bulk of spawning occurs in the coastal ocean, peaking during the winter off Cape Hatteras, North Carolina (Ahrenholz et al. 1987). However, some spawning is believed to take place throughout the species' range during most of the year (Nelson et al. 1977).

Massmann et al. (1962) proposed that spawning likely occurs over 64 km offshore based on the observations that while larger larvae occurred at greater abundance at stations closer to shore, in Virginia; in coastal waters there was an absence of eggs and smaller larvae. Following this work, cross-shelf transport dynamics were thought of as as the dominant process bringing larvae to nursery areas (e.g., Epifanio and Garvine 2001). Then, in the late 1990s, a multi-disciplinary effort known as the South Atlantic Bight Recruitment Experiment (SABRE) provided evidence from hydrodynamic modeling that

along shelf flow is the dominant process in delivering larvae and that inshore regions are the primary spawning sites (e.g., Hare et al. 1999, Checkley et al. 1999, Rice et al. 1999). Checkley et al. (1999) documented egg patches over 40 km from shore, but found near shore spawning was of higher importance based on hydrological conditions and model results.

Although general trends in spawning have been relatively well understood, more resent research has suggested different results of spatial variation of larval Atlantic Menhaden. Walsh et al. (2015) did not find significant changes in spatial distribution of larval Atlantic Menhaden when 1977 – 1988 was compared to 1999 – 2008. However, increasing relative juvenile abundance in southern New England estuaries (Buchheister et al. 2015) may suggest a northward shift spawning or suitable habitat for young menhaden. Alternatively, there may be different trends in early life mortality over space.

Long term changes in Atlantic Menhaden larvae were not uniform in time. Walsh et al. (2015) detected significant changes in the temporal distribution of Atlantic Menhaden larvae between 1977 – 1988 and 1999 – 2008 with more larvae occurring later in the season. In New Jersey, there has also been an observed shift in the timing of ingress, from a fall peak to June and July, since the late 1990s (Able and Fahay 2010).

The primary goal of this study was to assess changes in the pattern and timing of Atlantic Menhaden larval distribution. By examining the spatial distribution of different sizes of larvae, we were able to infer Atlantic Menhaden spawning locations and larval dispersal patterns. We used a spatial model of the smallest larvae to characterize the location and timing of spawning. Given higher abundances of all size classes of Atlantic Menhaden larvae nearshore (Simpson et al. *in review*) we expected to see the probability

of spawning to be greatest nearshore. Additionally, we expected spawning potential to increase southward, peaking offshore of North Carolina in the winter (Lewis et al. 1987, Stegmann et al. 1999). We performed a similar analysis to characterize the distribution of larger larvae to determine patterns of dispersal. Given the net southward flow of water near the coast in the Mid Atlantic Bight (Checkley et al. 1999), we expected the concentration of older larvae to increase southward, dispersing away from likely spawning locations.

Methods

Larval Data

Larval data were obtained from two National Oceanic and Atmospheric Administration (NOAA) sampling programs conducted on the U.S. Atlantic Coast: the Marine Resources Monitoring, Assessment, and Prediction (MARMAP) program and the Ecosystem Monitoring (EcoMon) programs. MARMAP was conducted during 1977-1987, and EcoMon, which began in 1992, is an ongoing program, although only ichthyoplankton samples from 1999 to 2013 were processed and available for this analysis.

The programs both used a stratified random sampling design, determined by depth and latitude. Ichthyoplankton programs were conducted on a roughly bimonthly basis from the U.S.-Canadian border, to Cape Hatteras, North Carolina. For more information on sampling procedures, see Chapter 2.

We restricted our analyses to tows conducted within the 25 strata in Southern New England and Mid Atlantic Bight regions because very few Atlantic Menhaden larvae were observed outside these regions. We paired months (Sept-Oct, Nov-Dec, Jan-Feb, Mar-Apr,

and May-Jun, Jul-Aug) to reflect the bimonthly sampling design. Tows conducted in July and August were excluded because no menhaden larvae were observed during July and only 15 were observed during August over the entire study period during both sampling programs (catches during the other months ranged from 1,468 to 304,931 individuals). September was treated as the beginning of the larval year such that larvae that hatched during September-December would be added to those from January through May of the following year to capture seasonal spawning dynamics.

Larval Size Distribution

We examined the size distributions of all larvae at each of the 25 strata sampled in southern New England and the Mid Atlantic Bight (Figure 3.1). Given the limited observations, tows were treated as replicates within each of the sampled strata. We calculated the mean and median sizes, as well as the range observed at each strata, and constructed corresponding histograms.

Estimating Spawning Locations

In order to address the question of spawning location and timing, only the smallest individuals collected in the programs were of concern. The cutoff we chose was 6mm. All larger individuals were excluded from this part of the analysis. Based on previous research on larval ingression in the Chesapeake Bay during the 2000s (Lozano et al. 2012), 6mm approximately corresponds to one week post hatch. During the MARMAP period, two years (1979 and 1980) and two bimonth categories (Jan-Feb and Mar-Apr) were removed due to zero positive observations of small Atlantic Menhaden larvae.

After removing the largest individuals, we reduced the abundance information to presence/absence because the abundance data were skewed with a large amount of zeros.

This simplification is appropriate for this analysis because our question is trying to address where and when larvae are occurring in order infer likely locations of spawning and general patters of dispersal. Further, we have some concern about a gear change from 505 µm mesh in the first program (MARMAP) to a 333 µm mesh in the second (EcoMon). Specifically, the smaller mesh size has been found to return greater abundances for fish below 9mm (Johnson and Morse 1994). The conversion to presence/absence helps reduce the effect of this change in retention.

We used a stochastic partial differential equation (SPDE; Lindgren et al. 2011) model in the R package INLA (Rue et al. 2009, Martins et al. 2012) to estimate areas and times of greatest spawning potential. The SPDE model allowed us to account for the spatial dependency inherent in spatially-structured data (Krainski et al. 2015). This approach approximates a continually indexed Gaussian field using a generalized covariance matrix (Besag 1981).

The first step of building this model is constructing a triangular grid over which the model will estimate spatial effects (i.e., mesh; Figure 3.1). We created a mesh over the entire area where samples were collected during the two programs. Within this boundary, we added triangles of uniform sizes. Next, we built a projector matrix which defines how the random field as well as other components of the model are linked to the response at the points specified by the vertices of the mesh. Specifically, the value for one point within one triangle is the projection of the plane (formed by these three weights) at this point location, i.e., a weighted average with the weights computed by the inla.spde.make.A() function.

We then ran a binomial model using the inla function from the INLA package

(Rue et al. 2009, Martins et al. 2012) of the above form, the data are paired with the locations from the projector matrix and we are able fit the following the model,

$$larv = \mu + M + Y + f(S) \qquad (3.1)$$

where larv was 0 or 1 based on absence or presence of small larvae in a tow, μ was the intercept, *M* was the bimonthly category (Sep-Oct, Nov-Dec, Jan-Feb, Mar-Apr, May-Jun) within which the tow took place, *Y* was the year (September through June), and *f(S)* was the spatial index. We assumed a normal error distribution.

Due to limitations in the number of observations over time, we were unable to include spatial and temporal interactions. In order to evaluate changes in temporal and spatial patterns between the two periods, we ran the model separately over both the MARMAP and EcoMon programs. The model provided mean estimates of the probability of occurrence of small larvae over time and space. Then, we calculated specific spatial estimates of probability of occurence over all months and years during both programs.

To identify areas with the highest probability of spawning activity, we ran SPDE models in INLA with the year factor removed. For each bimonthly category, we calculated estimates of spawning probability over the spatial range of sampling. Next, we compared these predicted values to the actual observations to construct receiver operating characteristic (ROC) curves corresponding to each bimonth category. From the ROC curves, we selected threshold values for each bimonth period to quantify annual and seasonal changes in likely spawning locations. This allows us to convert continuous probabilities to presence/absence predictions, in order to look at the total predicted occupied area.

Examining Larval Dispersal

Finally, we analyzed the presence-absence data for larvae > 6mm over our two study periods using the same models as were used for the small larvae. In this way, we were able to track where larvae approximately older than one week were transported post-spawning. We followed the same methods described for the smaller individuals.

Results

General summary

Both MARMAP and EcoMon ichthyoplankton programs were heavily sampled in the 25 strata covering the Mid Atlantic Bight (MAB) and Southern New England (SE) regions. From 1977 to 1987, 5,159 tows were conducted during MARMAP, and 3805 tows were conducted from 2000 to 2013, 3,805during EcoMon. There was a mean of 206 tows per strata and 152 tows per strata during MARMAP and EcoMon, respectively (Table 3.1). However, even with greater sampling in the earlier program, total abundance from all strata was 6.5 times higher in EcoMon than MARMAP, with 3.2 times higher total abundance in individuals greater than 6mm and 26.5 higher in individuals 6mm and smaller. There was a proportional shift in small versus large larvae in the two time periods. During MARMAP, small larvae made up 13.9% of total observed sizes, while during EcoMon, small larvae made up 57.0% of total observed abundance.

Similarly, when considering the number of tows with positive Atlantic Menhaden catches, EcoMon had 2.3 times greater positive tows than, MARMAP, with 2 times greater positive catch for individuals greater than 6mm and 5 times greater catch for individuals 6mm and smaller. Overall, 3.9% of tows conducted during MARMAP had positive menhaden catch compared to 12.4% of tows conducted during EcoMon. Excluding the northern most strata, near-shore strata demonstrated higher positive catch

and total abundance when compared to their offshore counterparts even after correcting for differences in sampling among strata. Near-shore strata were sampled an average of 129.4 times, compared to strata further from the shore sampled 242.6 times on average.

Size Distributions

The top 25% largest average (mean and median) sizes observed during MARMAP were at strata 3, 4, 6, 7, and 15. However, strata 4, 7, and 15 had low numbers of size observations with 1, 2, and 2, respectively (Table 3.2, Figure 3.2). Strata 3 and 6 make up the southern-most coastal sampling area, from south of Cape Hatteras, NC, to north of the Chesapeake Bay. The top 25% largest average (mean and median) size observations during EcoMon were at strata 3, 4, 10, 23, 24, and 25. Strata 3 is the only of these strata with adequate observations (>25) and is the southern-most strata off-shore of North Carolina. Strata 4 and 10, with 11 and 3 observations respectively, are outer shelf Mid Atlantic Bight strata. Strata 23, 24, and 25 are all northern strata, located south of Cape Cod, MA.

During MARMAP, the smallest median sizes (25^{th} quartile) were observed at strata 5, 9, 11, 23, and 24, or throughout the study area.The smallest mean sizes (25^{th} quartile) were observed at strata 5, 9, 11, 19, and 23 (Table 3.2, Figure 3.2). However, there were only 2 observations at both strata 19 and 23, and 11 observations at 24. The other strata with adequate observations (>25) were near-shore or adjacent between the Chesapeake and New York Bays. During EcoMon, the smallest median (25^{th} quartile) sizes were observed at strata 2, 6, 8, 12, 17 and 20 (Table 3.2, Figure 3.2). The smallest mean (25^{th} quartile) sizes were observed at strata 8, 12, 16, 19, 20, and 21. Strata 8 and 12 are the near-shore and adjacent strata closest to the mouth of the Delaware Bay, and

stratum 20 is mid-shelf near the tip of Long Island, New York. Strata 2, 6, and 17 all have smaller median than mean size observations, indicating a right skewed distribution. Stata 2 and 6 and southern strata, and 17 is offshore of New York Bay. Strata 16, 19, and 21 all have smaller mean than median size observations, indicating a left skewed distribution. These strata area all northern, near Long Island, NY.

Strata with the largest size ranges (difference between minimum and maximum, top 25%) were fairly consistent between the two ichthyoplankton sampling programs. During MARMAP, strata 3, 5, 9, 17, and 24 showed the greatest range in sizes. During EcoMon, strata 3, 5, 6, 9, 12, and 24 made up the top 25th quartile (Table 3.2, Figure 3.2). Strata 3, 5, and 9 are near-shore or adjacent strata south of Delaware Bay. Stratum 24 is a northern strata, but had only 11 and 12 size observations in MARMAP and EcoMon, respectively. Stratum 17, which had one of the largest size ranges during MARMAP, but not EcoMon, is coastal near New York Bay. Strata 6 and 12, which had two of the largest size ranges during EcoMon, by not MARMAP, are near Chesapeake and Delaware Bay, respectively.

Of the 25 strata included, 13 have more than 150 size observations over both ichthyoplankton programs, and the remaining 12 had 60 or fewer size observations (Table 3.2, Figure 3.2). We constructed histograms of size distributions for the 13 strata with more than 150 size measurements. Of the 12 strata with low observations, six of these were in the northern third of the study area, 3 in the middle third of the study area, and 3 in the southern third. The only two strata with adequate observations in the northern portion were the two strata nearest the mouth of Long Island Sound. The four included in the middle portion were those closest to shore. And, the seven included in the southern

portion were those closest to shore as well.

During both time periods, larval counts were highest in the southern third of the study area and lowest in the northern third (Figure 3.2). We also observed a trend in increasing maximum size and size ranges observed from north to south. The greatest difference between size distributions observed in the two programs is in overall magnitude. There were 3.8 times more larva measured during the more recent program. Further, the mean size observation was small in the more recent program, 8.3 mm compared to 11.5 mm. Similarly, there are not as many observed peaks at small sizes in the earlier MARMAP program compared to EcoMon. Otherwise, the size distributions are quite similar across the two programs. The primary exception to this was in strata 8, off-shore of the Delaware Bay. During the MARMAP program, there were few size observations, relative to other strata. Those observed had a somewhat bimodal distribution with modes around 5 and 15 mm. During the EcoMon program, we observed a heavily skewed right distribution with more size observations than any other strata.

INLA Models

We ran four models to characterize the spatial distribution of large and small larvae over the two periods. The models used between 2,619 and 5,159 observations. Sampling was more seasonally consistent during the EcoMon program than during MARMAP, which sampled considerably more during warmer months (Table 3.3). During both periods, there was a greater proportion of positive detections for large larvae than small. And, for both large and small larvae, there was a greater proportion of larvae detected in the later sampling program (Table 3.3).

We displayed mean effect of bimonth category of the probability of observing

larvae in a given tow as deviations from the mean. Any positive mean effect showed greater than average probability of detecting larvae, while any negative mean effect showed less than average probability of detecting larvae. Across all models, Nov-Dec had the greatest mean effect (Figure 3.3). For small larvae, during both time periods, Sep-Oct was second, followed by May-Jun. During the MARMAP program, Jan-Feb had the second greatest mean effect followed by both Sep-Oct and Mar-Apr (Figure 3.3). During the EcoMon program, Sep-Oct and Jan-Feb were tied for the second greatest mean effect, followed by Mar-Apr (Figure 3.3).

To illustrate the spatial patterns, we selected the years in which the probability of encountering larvae was greatest in each period (Figure 3.4) as results for other years had similar spatial patterns. Our model predicted consistently higher probabilities of encountering small larvae (6mm and smaller) throughout the sampling range during the EcoMon program (Figure 3.4). In both map predictions, there is a clear pattern of increasing probabilities of encountering small larvae towards shore. During MARMAP, there were hotspots in predicted probabilities near Long Island Sound, New York Bay, between the Chesapeake and Delaware Bays, as well as south of the Chesapeake Bay, with highest predictions near New York Bay. During EcoMon, hotspots where predicted in similar regions all near the mouths of major estuaries along the coast, but at consistently higher probabilities, and greatest probabilities projected along the Southern New England Coast and near the mouth of the Delaware Bay.

Each model separately estimated the mean spatial distribution of larvae over both year and bimonthly category. Thus, the projected probabilities for small and large larvae in two different periods showed the same patterns across months and years, but at different

intensities dependent on the mean effect of bimonth category and year, respectively. In order to best view spatial patterns, representative plots are shown for the times of greatest projected probabilities of detections. During both programs, there was higher predicted probabilities of observing larvae above 6mm (Figure 3.4c, d). Again, the greatest probabilities were predicted near-shore, but in a more continuous distribution along the coast. Highest abundance during MARMAP was concentrated in the southernmost portion of the range, south of Chesapeake Bay. During EcoMon, there was constantly high abundance from Long Island, New York through the southernmost area.

The ROC analysis showed mostly good model performance in both larval size groups, during both ichthyoplankton programs, according to the area under the ROC curve (AUC) (Figure 3. 5, Table 3.4). Year-bimonth combinations with more positive observations yielded smoother ROC curves. Cutoff values of the probability of larval presence in a tow determined from the ROC analysis ranged from 0.004 to 0.294 for all year-bimonth projections for all four models. Year-bimonth projections with greater numbers of positive observations yielded higher, thus stricter, cutoff values.

Comparing the proportional occupied area where we predicted small and large larvae, we observed a shift in which size class dominated the three regions (Figure 3. 6; northern: northern Long Island, NY, to Cape Cod, MA, middle: southern Long Island, NY, to north of Delaware Bay, southern: Delaware Bay to North Carolina). In the northern region, on average, we predicted small larvae to be present in 17.5% of the region during MARMAP and 9.3% of the region during EcoMon, compared to large larvae predicted in 9.0% and 6.1%, respectively. In either case, small larvae were predicted to occupy between 1.5 and 1.9 times more space than large. In the middle region, we predicted small

larvae to be present in 26.5% of the region during MARMAP and 33.4% during EcoMon, compared to large larvae predicted in 27.3% and 40.8%, respectively. Thus, in both surveys large larvae were modeled to be present in a greater area than small, but only slightly greater during MARMAP and 1.2 times greater during EcoMon. Finally, in the southern most region, we predicted small larvae to occupy 38.6% and 56.1% of the total area, during MARMAP and EcoMon respectively, compared to large larvae in 44.2% and 73.5%. In this region, large larvae take up 1.1 times more area during MARMAP and 1.3 times more area during EcoMon.

Comparing between the two periods, for both large and small larvae, we predicted Atlantic Menhaden to be present over a greater area overall during EcoMon. However, in the northern third portion of our study area this was not the case. In this region, we predicted the total area of likely larval Atlantic Menhaden occurrence to decrease between the early and later time period.

The area with predicted probabilities higher than the threshold values determined in the ROC curve increased from north to south for small larvae during both EcoMon and MARMAP programs. In both programs, interannual variation appeared to be greater than seasonal variation. During the MARMAP program (Figure 3. 6 a, c, d), Sep-Oct and Nov-Dec both resulted in very similar and the highest amount of area where they would be predicted to be present. May-Jun exhibited a similar pattern across years, but with a lower proportion of area predicted to have positive detections. Similarly, during the later program, there was a slightly different pattern in bimonth periods, Nov-Dec had the greatest proportion area coverage, followed by Jan-Feb, Mar-Apr, Sep-Oct, and May-Jun.

During the EcoMon program, predictions were more similar seasonally than

during the EcoMon program. During the MARMAP program, there appeared to be only three good years for small Atlantic Menhaden larvae: 1977, 1982, and 1983. However, during EcoMon, although there was considerable variation among years from 2000 to 2005, predictions were consistently high from 2006 onwards.

Similar to the models of the smallest larvae, both models applied to the larger larvae showed increasing areas of where they were likely to occur north to south. During both programs the predictions of proportional area were greatest during fall/winter (Sep-Oct, Nov-Dec, Jan-Feb) compared to spring and summer (Mar-Apr and May-Jun). During MARMAP, Jan-Feb showed higher predictions than Sep-Oct. However, this trend was reversed in the later EcoMon program. In 1977, predictions were moderate, in the southern region, just over 50 percent of the area was predicted to have large Atlantic Menhaden larvae present during the highest month. The next several years showed lower predictions, but with an increasing trend through the 1980s (Figure 3. 6e). On average, there was higher predicted areas of positive abundance during the EcoMon program. In the southern portion of the study area, during Nov-Dec, the model predicted from 43 to 99 percent of the area to likely contain larger larvae.

Discussion

Atlantic Menhaden spawning is likely occurring over an extremely large temporal and spatial range, and is not primarily concentrated off the coast of North Carolina, as some previous research has suggested (Lewis et al. 1987, Quinlan et al. 1999). Other studies have proposed that spawning occurs over a greater range (Nelson et al. 1977), as our work supports. More recently, there has been a shift in thinking that spawning was predominantly offshore, to predominately near-shore (Checkley et al. 1999, Hare et al.

1999, Rice et al. 1999, Stegmann et al. 1999, Werner et al. 1999). Checkley et al. (1999) also found that spawning in the Mid Atlantic Bight between the Chesapeake Bay and the Delaware had the largest contribution to larval ingress into North Carolina inlets. Our work shows this region to be an important spawning ground during both periods. Additionally, we found support of spawning hotspots even further north, near Long Island, NY. Although larvae were more commonly found during the early winter, there was some evidence of spawning throughout most of the year, excluding July and August.

The clearest gradient observed in our predictions was not north-south, but inshore-offshore. Both small and large larvae had considerably higher probabilities of detection closer to shore. However, large larvae were predicted over a smoother gradient along the coast, and a broader gradient away from the coast. This gives some evidence that spawning is most likely occurring near shore, with larvae transported both along and across the shelf. The most likely direction of transport is north to south (Quinlan et al. 1999). This theory may be supported by our observation of more large larvae relative to small in the southern portion of our study (Figure 3. 2). However, there are also likely differences in growth rates and mortality at different temperatures (Ferraro 1980).

Some earlier work has suggested a significant peak in spawning off the coast of Cape Hatteras, NC, in the winter (Higham and Nicholson 1964, Kendall and Reinjes 1975, Judy and Lewis 1983). While we found a broad trend of increasing small larvae southward, we did not see evidence of such a dramatic peak. Although, we may be missing some critical information due to our lack of observation south of Cape Hatteras, North Carolina. During the MARMAP program, the coastal waters south of New York were predicted to have the greatest probability of larval occurrence. During EcoMon, the greatest probability

of detection was near Delaware Bay and Long Island, NY.

However, we did find the southern-third of our spatial range, from just north of Delaware Bay to Cape Hatteras, NC, to have the greatest total area of which spawning was likely to occur. And, the majority of detections took place during November and December. Thus, the species' southward winter migration is likely an important time for spawning (Ahrenholz 1991).

Since the mid-2000s, when the Atlantic Menhaden population is believed to have recovered, the occupied area of both large and small larvae has been consistent. This suggests that a healthy adult biomass is the most important factor in insuring high larval supply (Warlen 1994).

Occupied area of small larvae was quite variable among years prior to 2006. However, from 2006 to 2013, the total area predicted to have small larvae stayed fairly constant. We believe this is due to the recovery of the adult population, particularly the recovery of a full age-structure. From 2006 onwards, fishing mortality remained constant and low while the adult biomass was estimated to be higher than it has been in the past several decades (Figure 3. 7; SEDAR 2015). Our work supports the findings by the most recent assessment that the population is not being overfished in such a way that recruitment is being limited by adult abundance.

Occupied area of large larvae, though echoing the same general annual trends as the small larvae, shows less variation among years. Even in years where no small larvae were observed (1979, 1980), near 25% of the southern region was projected to have large larvae present. In years where spatial coverage of small larvae was greatest, the spatial coverage of large larvae was projected to be similar. Larger larvae are expected to disperse away

from spawning locations as they develop, as to decrease competition as well as mortality by adults (Shanks 1995). Thus, we expect large larvae would disperse away from spawning locations. Larvae ingressing into Chesapeake Bay in a study conducted from 2009 to 2011 found ages ranging 9 to 96 days with an average of 44-50 days post-hatch (Lozano et al. 2012). It is a common observation in fish and invertebrate larvae that while small individuals are found closest to shore, larger individuals are observed almost exclusively farther from the coast (Shanks 1995). While we did not observe such an exclusion of larger larvae near the coast, we did see high probabilities of encountering large larvae further from shore than small larvae. Increased abundance of large larvae away from nursery habitats may be favorable because advection into coastal estuaries before larvae have developed swimming abilities would make them highly susceptible to predation in the more productive nursery areas. However, larvae simultaneously must remain near enough to shore to be able to eventually ingress. Although larval fish are unlikely to be able to control their location by horizontal swimming alone, they can exert some control through vertical movement by occupying different depths (Shanks 1995).

Of course, even in years where we observed zero small Atlantic Menhaden larvae, we know that there were still many present. Our study is limited by the spatial extent of the sampling programs. Shallow near-shore water is likely to be important spawning ground given the general pattern of increased probability of encountering small and large larvae near shore. However, areas closest to shore were not sampled in either program due to vessel limitations. Although traditionally thought of as coastal spawners (Ahrenholz 1991), eggs have been found in northern estuaries (Keller et al. 1999) suggesting some spawning may also be occurring within such estuaries. Additionally, the programs we studied only

extended as far south as Cape Hatteras. Historically, the Chesapeake Bay has been thought to be the most important nursery habitat for juvenile Atlantic Menhaden (Ahrenholz et al. 1989, ASMFC 2004, Anstead and Jones 2014). Given the north to south near-shore current, we would expect the bulk of larval supply to be coming from the north. Although, more spatial coverage south would be beneficial to this analysis, giving us confidence that we covered the majority of the important spatial range.

Examining both small and large larvae over the three distinct regions (north, middle, and south) we were able to compare how large and small larvae occupied space. Our observation in a shift from small larvae occupying relatively more space in the north to large larvae occupying relatively more space in the south could be explained by several factors. Although some research has speculated that Atlantic Menhaden larvae may be transported northwards along the coast (Warlen et al. 2002), hydrodynamically it is more likely that larvae are net transported southwards in the Mid-Atlantic Bight (Quinlan et al. 1999). Given a net southward movement of larvae, we would not expect to see great numbers of larvae in the northern portion of our study area, as there would be limited larval supply coming from further north. The middle and southern regions could receive larvae from the north in addition to individuals spawned nearby. This effect would be cumulative moving south, particularly for large larvae. Additionally, there may be differences in survival. A higher level of mortality in the northern region would also contribute to observing small larvae occupying more space.

Due to low numbers of observations, we were unable to examine month-to-month or year-to-year changes in space. The model results we have shown represent an average spatial distribution during each of the two time periods among months and years. Given

more information, it would be informative to examine how spatial distribution changes over time. Atlantic Menhaden are known to exhibit high levels of variability among years, particularly in terms of recruitment (eg; Vaughan and Merriner 1991, Keller et al. 1999, Warlen et al. 2002). Even still, our research supports previous work showing no major directional change in spatial distribution of larvae between the two time periods (Walsh et al. 2015). This was true for both small and large larvae, indicating no major spatial shift in spawning or dispersal.

Walsh et al. (2015) did find a temporal shift in the presence of larvae. Although, during both periods, early winter is when the majority of larvae were observed, we found evidence for an increase in spring spawning during the more recent period. Similarly, we observed more large larvae during the spring in the more recent program. This may partially explain the observed shift in peak larval ingress to New Jersey estuaries from fall to early summer after 1990 (Able and Fahay 2010).

The two periods we examined represent two distinct patterns of recruitment, particularly to the Chesapeake Bay. During the MARMAP program, adult biomass was generally lower and juvenile abundance was high in the Chesapeake Bay. During the EcoMon program, adult biomass increased, but juvenile abundance remained low (SEDAR 2015). One hypothesis proposed to explain the poor recruitment to the Chesapeake Bay was poor larval supply (Houde et al. 2011). We found no evidence of this. In fact, more recently, larval supply should have only improved. Not only did we observe more larvae overall, we observed more larvae over a larger range of months. We also saw a major increase in probability of encountering larvae just north of the Chesapeake Bay, the direction from which we would expect larvae to be transported.

Recent research in the Chesapeake Bay has indicated that although the bulk of larvae is ingressing in the winter, surviving juveniles were more often hatched in the spring (Lozano et al. 2012). One proposed mechanism for this observation is that individuals hatched in spring, encounter more favorable growing conditions as larvae, a fitness that continues into their juvenile life stage (Atkinson and Secor 2016). Therefore, in order to have a complete understanding of recruitment, we must have a better understanding of factors affected early life survival.

The patterns we observed is closely related to what has been described as 'bet-hedging', which relies on the idea that some success across many years is evolutionarily more beneficial to the species than high success in some years and low success in others (Phillipi and Seger 1989). Traditionally, bet-hedging refers to phenotypic variation in offspring. The sort of bet-hedging we see in Atlantic Menhaden is mechanistically different. It is not so much the diversity of offspring that is relevant, but rather the diversity of conditions these offspring are exposed.

Tables and Figures

Table 3.1. Summary of abundance and number of positive catch of larval Atlantic Menhaden by plankton stratum for two size classes (small: 0-6mm, large: >6mm). Total tows conducted and mean latitude and longitude sampled within each strata are also shown. Columns with the "M" header show information from MARMAP (1977-1997), and columns with the "E" header show information from EcoMon (2000-2012). Strata closest to shore are in bold.

					Small				Large			
			Tows		Abundance		# Positive		Abundance		# Positive	
Strata	Lat	Lon	M	E	M	E	M	E	M	E	M	E
1	-74.83	36.05	75	64	0	8.32	0	2	20.69	65.05	3	8
2	-75.15	36.10	126	131	30.52	681.4	2	14	967.71	469.53	9	31
3	**-75.46**	**35.86**	**145**	**97**	**48.17**	**68.02**	**3**	**9**	**651.44**	**703.49**	**24**	**25**
4	-74.64	37.21	127	90	0	6.16	0	1	6.91	35.88	1	5
5	-75.15	37.12	408	323	392.08	2340.89	8	30	1809.09	6585.4	17	37
6	**-75.70**	**37.00**	**164**	**114**	**2.62**	**4015.93**	**1**	**19**	**187.33**	**1217.94**	**19**	**31**
7	-74.01	38.04	213	152	0	0	0	0	11.7	45.39	2	6
8	-74.48	38.38	387	263	13.05	8115.88	1	35	68.14	2289.94	6	45
9	**-75.11**	**38.01**	**113**	**59**	**158.26**	**292.61**	**4**	**8**	**433.71**	**404.45**	**8**	**16**
10	-73.15	38.89	136	176	0	0	0	0	0	15.54	0	3
11	-73.73	39.24	266	242	19.17	4776.19	3	18	75.47	1603.76	9	32
12	**-74.78**	**38.81**	**98**	**52**	**3.59**	**451.3**	**1**	**12**	**46.85**	**131.23**	**4**	**15**
13	**-74.09**	**39.60**	**219**	**106**	**57.25**	**2272.36**	**5**	**13**	**349.9**	**2051.87**	**18**	**35**
14	-72.16	39.56	154	78	0	0	0	0	0	0	0	0
15	-72.61	39.78	295	250	0	88.12	0	7	11.62	153.76	2	9
16	-73.12	40.22	400	268	169.28	734.77	8	27	471.3	1988.44	26	30
17	**-73.41**	**40.49**	**179**	**61**	**10.75**	**988.45**	**3**	**12**	**265.97**	**580.85**	**15**	**21**
18	-70.87	40.08	131	77	0	0	0	0	0	0	0	0
19	-71.39	40.44	334	296	6.55	18.41	1	2	5.02	43.52	1	2
20	-71.48	41.00	307	210	16.74	302.9	3	17	321.16	159.46	13	15
21	**-71.74**	**41.07**	**62**	**42**	**8.39**	**238.45**	**2**	**11**	**173.22**	**577.12**	**5**	**8**
22	-69.59	40.07	91	77	0	6.2	0	1	0	4.6	0	1
23	-69.62	40.48	437	315	5.33	0	1	0	5.1	16.16	1	3
24	-70.10	40.88	237	198	16.99	5.1	2	1	34.53	33.42	5	6
25	**-69.93**	**41.17**	**55**	**64**	**0**	**0**	**0**	**0**	**0**	**22.8**	**0**	**1**

Table 3.2. Summary of larval Atlantic Menhaden length information from tows conducted at 25 plankton stratum on the Atlantic coast during MARMAP (1977-1987) and EcoMon (2000-2013) sampling programs. Bold rows have corresponding histograms displaying actual size distributions (Figure 3.2).

	MARMAP						EcoMon					
STR	n	median	mean	sd	min	max	n	median	mean	sd	min	max
1	3	12	11.43	4.97	6.2	16.1	15	10.1	12.21	5.10	3.8	19
2	**165**	**12**	**12.46**	**4.52**	**5.3**	**23.1**	**342**	**6.75**	**8.42**	**5.53**	**2.6**	**23**
3	**254**	**20.15**	**17.89**	**6.43**	**4**	**29.9**	**348**	**14.6**	**13.99**	**5.80**	**2.5**	**25.2**
4	1	16.5	16.50	NA	16.5	16.5	11	14	12.81	5.61	4.7	19.8
5	**369**	**7.6**	**9.32**	**5.29**	**3.1**	**24.5**	**1037**	**7.8**	**7.78**	**3.34**	**2**	**23**
6	**134**	**17.9**	**16.47**	**4.80**	**4**	**25**	**777**	**5**	**8.27**	**6.22**	**2**	**24**
7	2	14.2	14.20	7.21	9.1	19.3	11	11.3	11.48	3.10	8	18
8	**23**	**11**	**10.62**	**4.31**	**4.5**	**17.5**	**1167**	**5.5**	**6.84**	**3.85**	**1.6**	**22**
9	**164**	**7.35**	**7.91**	**3.14**	**3.2**	**26.5**	**230**	**10**	**11.25**	**6.90**	**2**	**25**
10	0	NA	NA	NA	NA	NA	3	14	16.00	5.29	12	22
11	**30**	**7.6**	**8.89**	**3.70**	**4.8**	**20.5**	**649**	**10.6**	**9.34**	**4.11**	**1.1**	**21.8**
12	**28**	**10.25**	**13.13**	**6.16**	**6**	**25**	**289**	**4**	**5.31**	**3.67**	**1.8**	**26**
13	**157**	**9.5**	**9.46**	**3.19**	**3.5**	**20.5**	**520**	**8.1**	**8.67**	**4.60**	**2**	**22.3**
14	0	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
15	2	15	15.00	9.90	8	22	58	7.1	7.86	3.54	2.7	19.8
16	**126**	**9.25**	**9.75**	**3.84**	**3**	**23.6**	**439**	**7.7**	**7.72**	**3.00**	**3**	**17**
17	**98**	**10.6**	**11.64**	**4.11**	**3.1**	**31**	**331**	**6.5**	**7.91**	**4.29**	**2.5**	**21**
18	0	NA	NA	NA	NA	NA	0	NA	NA	NA	NA	NA
19	2	9.4	9.40	5.09	5.8	13	13	7.8	6.85	2.30	3.2	9.7
20	**92**	**10**	**10.80**	**3.26**	**3.8**	**21.5**	**137**	**4.2**	**5.75**	**3.25**	**2.6**	**21**
21	**48**	**10.6**	**11.50**	**3.52**	**5.4**	**18**	**130**	**7.1**	**6.89**	**3.52**	**2.7**	**20**
22	0	NA	NA	NA	NA	NA	2	10.65	10.65	6.86	5.8	15.5
23	2	8.9	8.90	5.80	4.8	13	3	22	22.00	7.50	14.5	29.5
24	11	7.2	10.78	7.33	4.3	26	12	24	20.57	11.35	5.1	32
25	0	NA	NA	NA	NA	NA	4	25.5	25.63	6.26	18.5	33

Table 3.3. Sample sizes, number of tows with positive detections, and percent positive by month and in total for each of the four INLA models run for large and small Atlantic Menhaden larvae during MARMAP (1977-1987) and EcoMon (2000-2013) sampling programs.

		Sep-Oct	Nov-Dec	Jan-Feb	Mar-Apr	May-Jun	Total
small MARMAP	n	797	601	NA	NA	1221	2619
	positive	13	33	NA	NA	2	48
	%	**1.6**	**5.5**	**NA**	**NA**	**0.2**	**1.8**
small EcoMon	n	770	786	685	778	786	3805
	positive	68	130	3	5	33	239
	%	**8.8**	**16.5**	**0.4**	**0.6**	**4.2**	**6.3**
large MARMAP	n	976	648	480	1563	1492	5159
	positive	19	101	36	28	4	188
	%	**1.9**	**15.6**	**7.5**	**1.8**	**0.3**	**3.6**
large EcoMon	n	770	786	685	778	786	3805
	positive	73	202	57	34	19	385
	%	**9.5**	**25.7**	**8.3**	**4.4**	**2.4**	**10.1**

Table 3.4. Sensitivity, specificity, AUC (area under the ROC curve), and cutoff values for each of the four INLA models and for each bimonthly factor included in the models.

		Sep-Oct	Nov-Dec	Jan-Feb	Mar-Apr	May-Jun
Small MARMAP	sensitivity	0.846	0.879	NA	NA	1.000
	specificity	0.688	0.762	NA	NA	0.871
	AUC	0.816	0.866	NA	NA	0.918
	cutoff	**0.022**	**0.083**	**NA**	**NA**	**0.004**
Small EcoMon	sensitivity	0.809	0.846	0.667	1.000	0.970
	specificity	0.717	0.738	0.636	0.660	0.752
	AUC	0.810	0.861	0.538	0.745	0.901
	cutoff	**0.128**	**0.218**	**0.005**	**0.008**	**0.066**
Large MARMAP	sensitivity	0.737	0.881	0.750	0.786	1.000
	specificity	0.717	0.775	0.658	0.859	0.935
	AUC	0.741	0.866	0.774	0.866	0.966
	cutoff	**0.023**	**0.201**	**0.073**	**0.035**	**0.007**
Large EcoMon	sensitivity	0.795	0.837	0.737	0.824	0.842
	specificity	0.633	0.791	0.739	0.788	0.777
	AUC	0.775	0.870	0.785	0.821	0.874
	cutoff	**0.079**	**0.294**	**0.114**	**0.071**	**0.039**

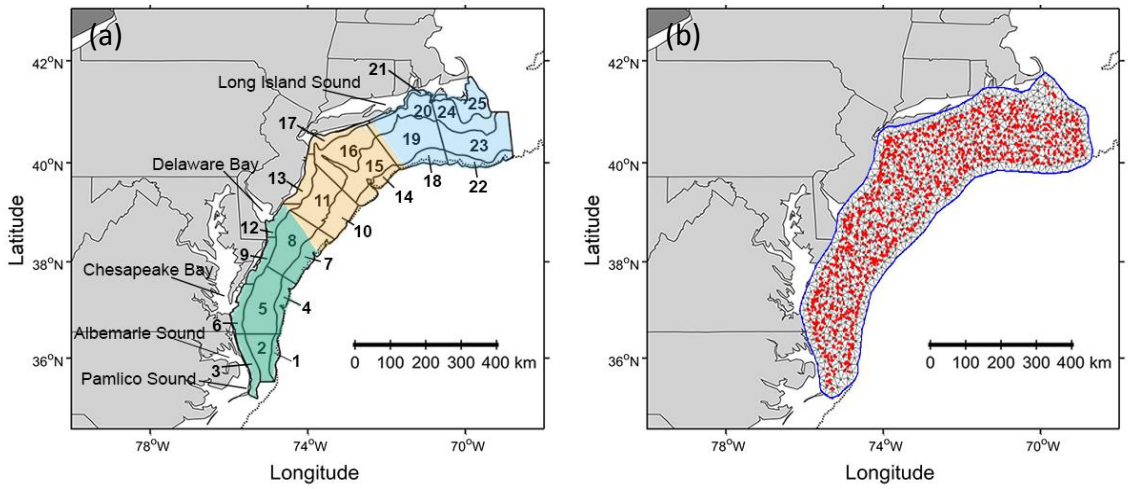

Figure 3.1. (a) Plankton strata included in spatial analysis. Blue, yellow, and green colors correspond with northern, middle, and southern thirds of sampled area and to Figures 3.2 and 3.6. (b) The triangular mesh constructed in INLA used for the SPDE models on MARMAP (1977-1987) and EcoMon (2000-2012) for the characterization of Atlantic Menhaden spawning activity. Red points designate locations of tows conducted during both periods.

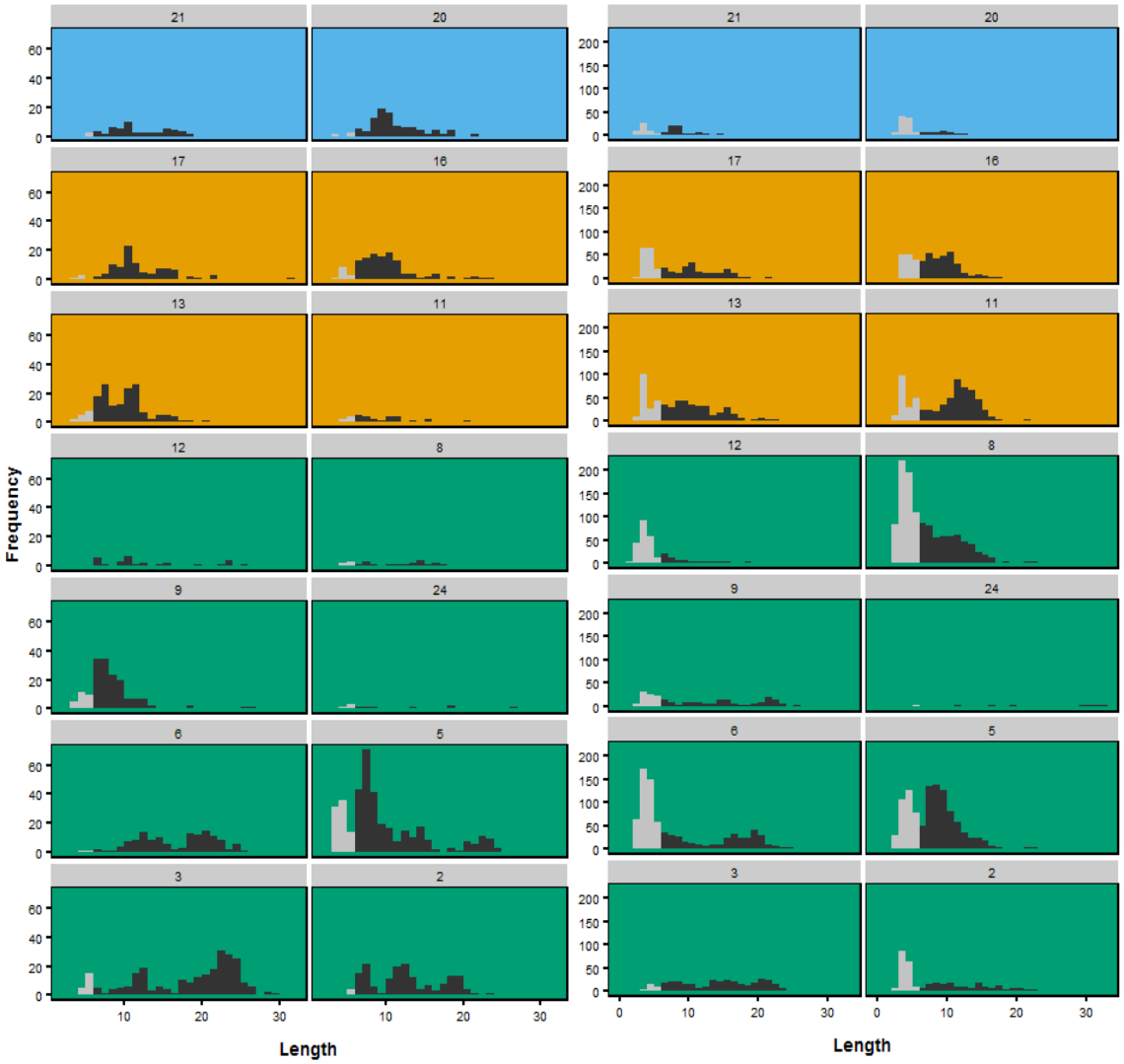

Figure 3.2. Frequency distributions of all sizes observations of larval Atlantic Menhaden at each strata from the MARMAP and EcoMon icthyoplankton programs. Grey bars show larvae 0-6mm, and black show larvae >6mm. Blue, yellow, and green backgrounds indicate strata in the northern, middle, and southern third of our study area, respectively (Figure 3.1a).

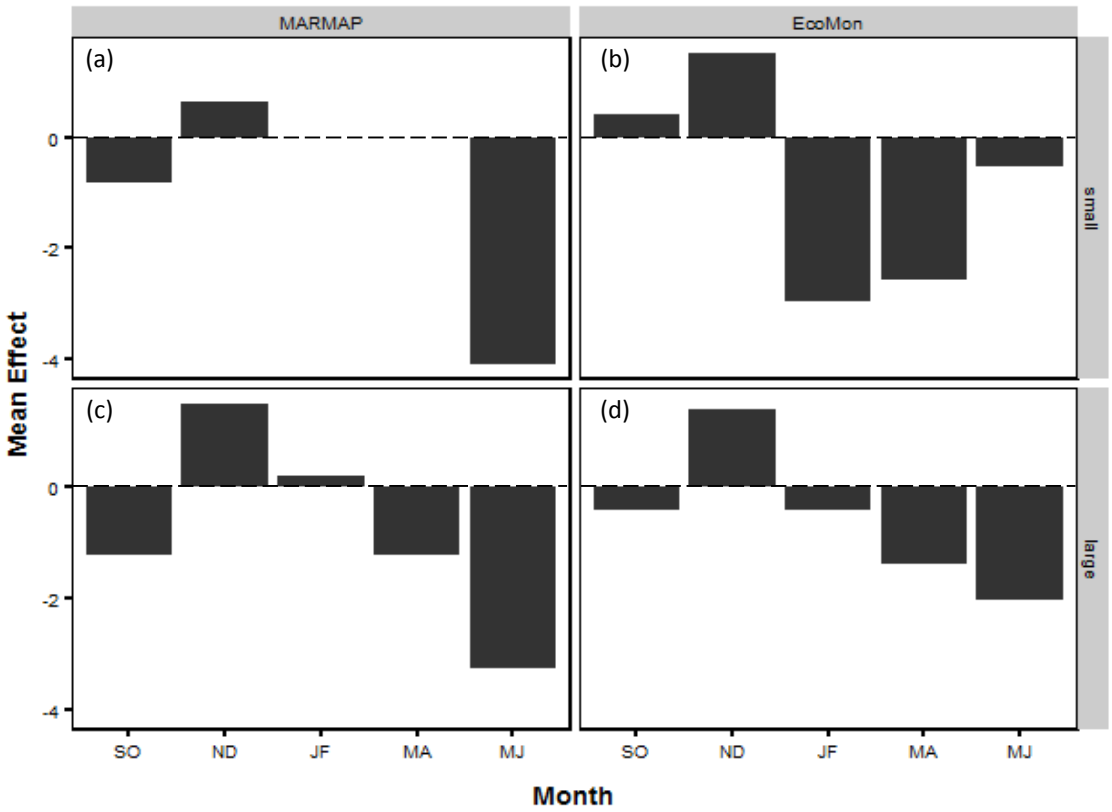

Figure 3.3. Mean effect by bimonthly category (SO: Sep-Oct, ND: Nov-Dec, JF: Jan-Feb, MA: Mar-Apr, MJ: May-Jun) from the four INLA models applied to larval Atlantic Menhaden presence/absence data obtained from MARMAP (1977-1987) and EcoMon (2000-2013) sampling programs. (a) larvae 0-6mm, MARMAP (b) larvae 0-6 mm, EcoMon (c) larvae >6mm, MARMAP (d) larvae >6mm, EcoMon.

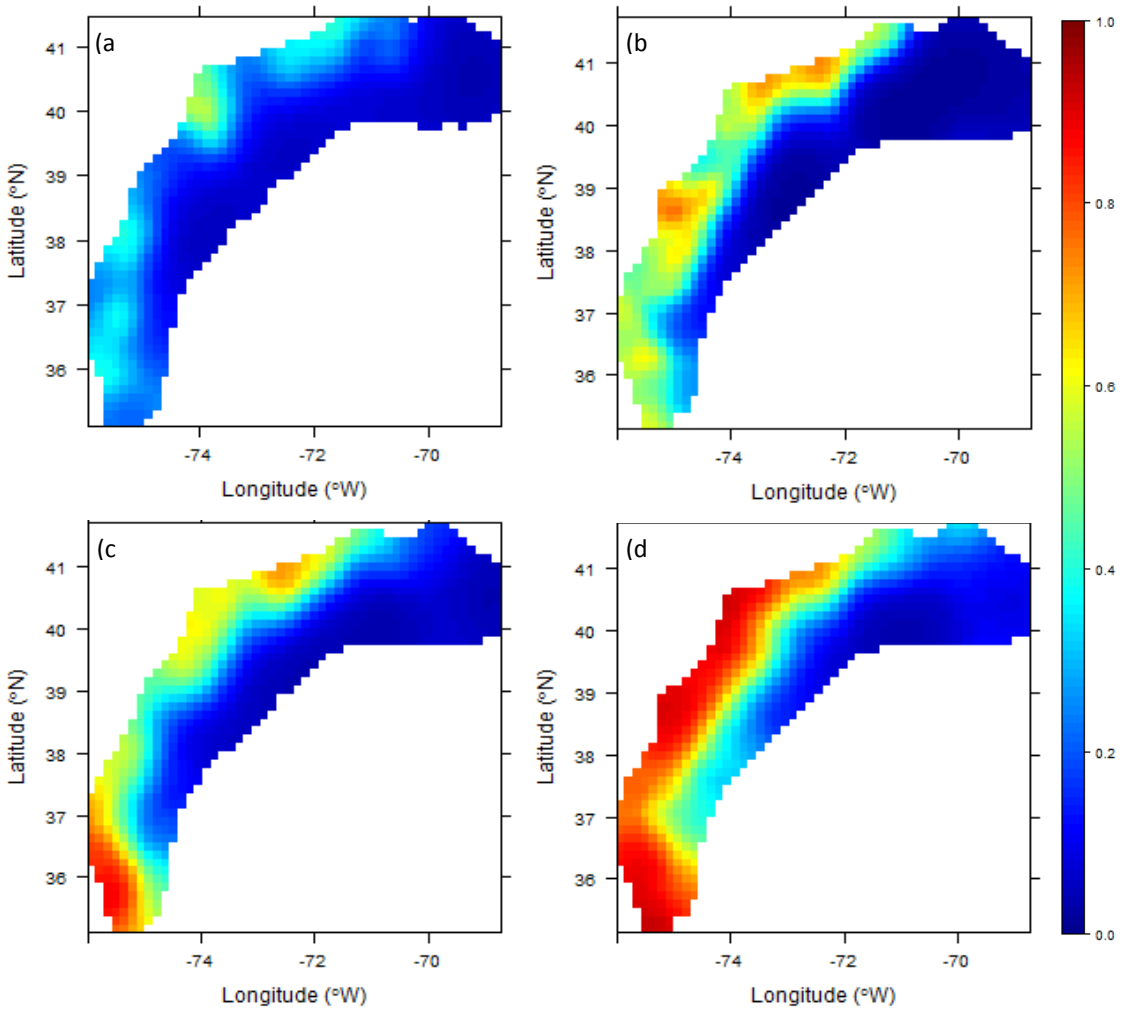

Figure 3.4. Normalized probability of the occurrence of Atlantic Menhaden larvae during November and December from four INLA models applied to data collected from MARMAP (1977-1987) and EcoMon (2000-2013) sampling programs. (a) larvae 0-6mm (1977) (b) larvae 0-6 mm (2004) (c) larvae >6mm (1985) (d) larvae >6mm (2004).

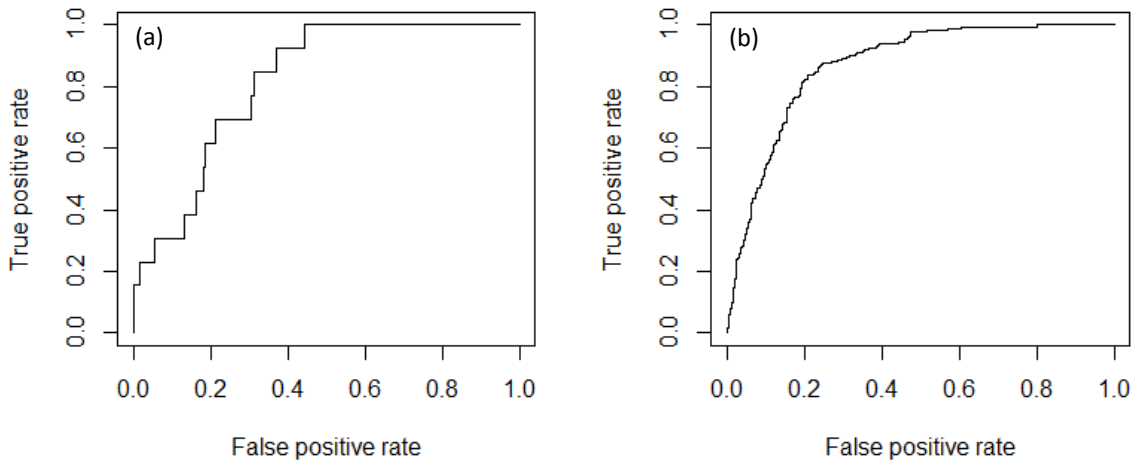

Figure 3.5. Example ROC curves created to determine cutoff values for presence/absence of small and large Atlantic Menhaden larvae during MARMAP (1977-1987) and EcoMon (2000-2013) ichthyoplankton surveys for 5 bimonth periods. (a) Small (0-6mm) larvae during Sep-Oct from MARMAP (b) large (>6mm) larvae during Nov-Dec from EcoMon.

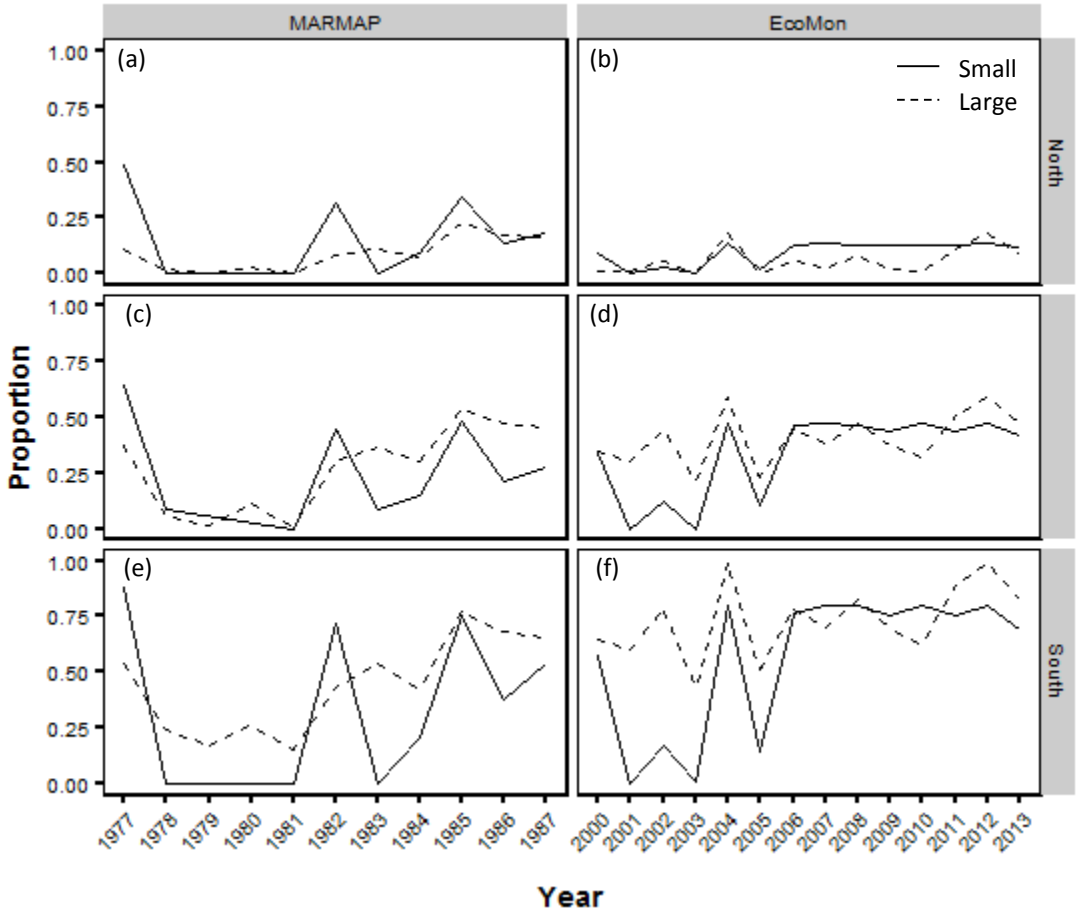

Figure 3.6. Proportion of region (North to South) predicted to have small (0-6mm; solid line) and large (<6mm; dashed line) larvae during both MARMAP (1977-1987) and EcoMon (2000-2013) sampling programs based on results of four SPDE models. (a) MARMAP, northern third of the study range. (b) EcoMon, northern third of the study range. (c) MARMAP, middle third of the study range. (d) EcoMon, middle third of the study range. (e) MARMAP, southern third of the study range. (f) EcoMon, southern third of the study range.

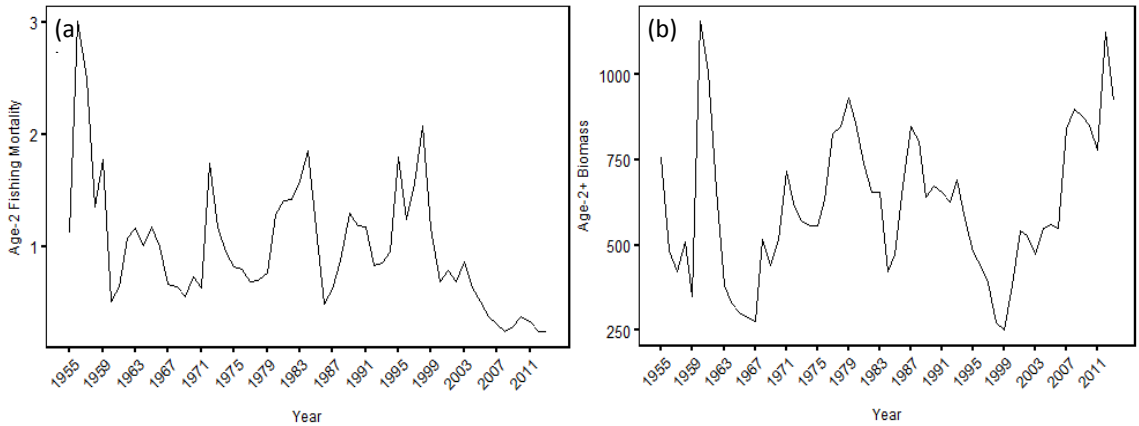

Figure 3.7. Fishing mortality and biomass of Atlantic Menhaden from most recent stock assessment (SABER 2015). (a) Age-2 fishing mortality. (b) Total biomass of ages 2 and older.

Chapter 4: Conclusion

In this work, we observed an overall increase in Atlantic Menhaden larval abundance over time. However, we simultaneously observed a decrease in early life survival. While we were not able to identify any definite causes of such a decline, variation in coastal temperature, Atlantic Multidecadal Oscillation, and wind speed all may offer at least partial explanations. General patterns of near-shore and southward increasing spawning area and larval dispersal were fairly consistent between the two examined periods. Although, despite a decrease in early life survival, we observed an expansion of occupied area of both large and small larvae over time.

This research was made possible by two long term ichthyoplankton sampling programs conducted by the National Oceanic and Atmospheric Administration (NOAA). These sampling programs operated on the Atlantic Coast, north of Cape Hatteras, NC, beginning in 1977. Scientifically surveys of this temporal and spatial range are rare, but extremely valuable, in fisheries sciences. Surveys of this magnitude allow scientists and managers to assess broad-scale patterns in populations. With such information, it may become possible to detect patterns not obvious on more localized or shorter time scales. Similarly, it allows managers to test to see if previously observed, localized patterns have a long-term or population level effect.

This project was proposed in order to address concerns related to Atlantic Menhaden recruitment. The adult spawning stock is considered not overfished, with no overfishing occurring. However, juvenile abundance in nursery habitats has declined in the past decade. One proposed explanation for poor recruitment is poor larval supply. In this work, we found that larval abundance had increased and that it corresponded closely with adult biomass. Additionally, larvae were observed over a larger spatial distribution in years post-recovery. This indicates that the abundant larval supply is exposed to a greater range of conditions in productive years. While this may lead to a lower proportion of surviving individuals, we would expect to see a corresponding

increase in juvenile abundance.

Instead, we observed a negative relationship between larval and juvenile abundance. If poor recruitment cannot be explained by larval supply, it must be caused by some combination of: transport failure, larval mortality, and juvenile mortality. Again, we found the spatial range of small and large larvae to be consistently highest in the past decade. This indicates that spawning is occurring over a great range, and also that larvae are dispersing over a great range. In recent years, we found larvae to be abundant near Delaware Bay, an area they were rarely detected during 1977-1987. Although it is possible that larvae are not being properly transported into estuaries, we still detected highest probabilities of encountering large larvae nearshore, and thus near nursery habitats. Overall, we found more recent conditions to better favor successful ingress.

It seems that the two most likely explanations for declining Atlantic Menhaden recruitment are increased larval mortality and increased juvenile mortality. We observed early life survival (from coastal larvae to estuarine juvenile) to be decreasing overtime, particularly since 2000. We tested six environmental factors against early life survival. Of those, AMO, coastal temperature, and Chesapeake Bay mouth mean annual wind speed may have an effect. While it is likely that other environmental factors affect Atlantic Menhaden at theses life stages, because the population occupies such a large spatial distribution, localized conditions are difficult to account for on a coastal scale.

While we did not calculate larval mortality directly, we can draw some conclusions on the subject from our spatial analysis. We modeled probability of detecting small and large larvae over two periods. Although the projected probabilities were much higher during the more recent period for both large and small larvae, this difference was not as great for the large larvae, although some of this may be attributed to a change in mesh sizes. Thus, even with a reduced spawning stock and larval supply, the probability of encountering large larvae was similar to what it is in the more recent time period. Examining spatial distribution of large and small larvae, large larvae exhibit much less interannual variation compared to small. Although spatial range is not

the same as abundance, our findings suggest compensatory dynamics early on with greater larval survival in years where larval supply was low.

If such dynamics are at play, this would help explain declines in early life survival in recent years. However, because even if recent years have experienced reduced larval survival, overall larval abundance has increased, and spatial distribution of large larvae has remained constant.

Therefore, we believe that future research in this area should be focused on survival from coastal larvae to estuarine juveniles. Our work has begun identifying mechanisms to explain factors that may be affecting population-wide reduced recruitment. However, there is potential to expand on this research. We suggest conducting a multivariate analysis of environmental conditions for comparison against our larval data in an effort to determine specifically what combinations of conditions, if any, best favors high larval abundance. In order to better address the gap in knowledge concerning survival from larva to juvenile, more work can be done within estuaries tracking ingress. This should be conducted year-round, not just during the peak season in order to accurately gauge larval transport into estuaries and provide a baseline for within estuary juvenile survival.

Currently, all evidence suggests that Atlantic Menhaden are an extremely resilient species. They have been heavily exploited for over a century, and have rebounded on several occasions. They are able to do this because of their highly productive, bet hedging life history. They produce massive numbers of larvae annually over as great of spatial and seasonal scale as possible. In doing such, they expose their young to a wide array of environmental conditions. Although the vast majority of their young will die before getting the chance to metamorphose into juveniles, chances are, a healthy number will survive. This strategy works particularly well in a dynamic and highly variable environment, such as the Atlantic coast. However, the continued low recruitment should still be a source of concern. Understanding mechanisms behind this phenomenon could only lead to improved management and help prevent future population

declines.

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